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Taphonomy and Palaeoecology of multi-element skeleton invertebrates: a genetic model for exceptional preservation

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Abstract

The aim of the research is to improve the understanding on the origin of fossil accumulations by investigating their taphonomic and sedimentological features and by using stratigraphic data and the autecology of the organisms forming the shell beds.

A number of highly different oligospecific high dense fossil accumulations of well-preserved, multi-element skeleton invertebrates, such as arthropods and echinoids, were studied.

The first case studied concerns the Ordovician trilobite-like arthropod *Tariccoia arrusensis,* which is found locally within the grey siltstones of Riu Is Arrus Member (Monte Argentu Formation, Upper Ordovician), cropping out along the valley of the creek Riu Is Arrus, SE Fluminimaggiore (SW Sardinia). The locality Roia Srappas is the most distinctive whit regards to the fossil content. The facies analysis allows documenting a clastic sequence whose origin is related to turbidity currents (hyperpycnal flows) generated by a flood-dominated fluvio-deltaic system entering in lagoonal or protected shallow marine settings. Two taphofacies are recorded: tf1 consists of a high density of articulated remains, which constantly show convex down orientation, while tf2 consists exclusively of disarticulated remains randomly oriented. The preservation state and preferred orientation of arthropods in the tf1 leads to infer gentle transport by mud plumes, related to hyperpycnal flows, rapid burial and low scavenging and bioturbation.

The second case focused on four clypeasteroid mass occurrences from the Lower Miocene of Sardinia, which are analyzed and compared. Two clypeasteroid assemblages were found within the Nurallao Formation (Late Oligocene-Burdigalian). The other two investigated clypeasteroid assemblages that were investigated, are found within the Calcari di Mores Formation (Late Burdigalian). These fossil echinoid deposits show a

low taxonomic diversity: two assemblages are dominated by the genus *Amphiope* while the other is dominated by *Parascutella* with subordinate *Clypeaster*. Although the four sand dollar deposits, which are the object of this study, can be assigned to a shoreface environment, there are differences in their features and origin. Three different genetic mechanisms, such as multiple in situ reworking, storm deposition and autochthonous accumulation can be inferred.

The third case focused on regular echinoid and spatangoid mass accumulations, which are extremely rare in the fossil record of the Miocene of Sardinia. In the Lower Burdigalian sediments of the Marmilla Formation two monospecific regular echinoid and spatangoid mass occurrences were found. The regular echinoid assemblage consists of a dense accumulation of phymosomatid echinoid *Anisophyma* n.g.n.sp., which is decribed and illustrated. The other echinoid assemblage is a monospecific *Brissopsis* beds. The third regular echinoid mass accumulation, which is found within the Gesturi Marls (Upper Burdigalian to Langhian), is a sea urchin spine bed with rare and poorly-preserved complete tests. Although the three studied echinoid mass accumulations can be trace to a storm-dominated offshore environment, observed variations in the taphonomic and sedimentologic features are due to three different genetic mechanisms such as, rapid buried living community (obrution), time-averaged fossil bed by sediment starvation, and distal tempestite event. The studied mass accumulations allowed explaining the nature and the distribution of the fossil concentrations across a wide spectrum of environments. Nearshore depositional environments are dominated by sedimentological concentrations but can also include sedimentologically overprinted biological concentrations. In deeper water environments shell-bed development can mainly be the results of ecologic (biologic) mechanisms, shell accumulation during episodes of sediment starvation and rapid burial by storm events. The analysis of multi-

element skeleton mass accumulations showed that these fossil deposits are a useful tool for palaeoenvironment and palaeoecological reconstructions.

Keywords: Taphonomy, sedimentology, palaeoecology, arthropods, echinoids, mass accumulations.

Introduction

Aims of the work

The fossil material is not uniformly distributed in the sedimentary record but is concentrated on all scales, from single bedding plane to basinwide deposits (Kidwell, 1986). Obviously palaeontologists are inclined to focus their taxonomic and palaeoecologic investigations on the richest parts of the fossil record. Therefore it is very important to study fossil concentrations at high level of confidence with the aim of clarify their features, peculiarities and origin. In fact an understanding of the formation of fossil accumulations is vital in interpreting the nature and biases of the fossil record.

The pioneering contributions provide by Johnson (1960), Schäfer (1972), Fursich (1978) and Kidwell (after 1982) laid the groundwork for the subsequent studies to the understanding of the origin of fossil concentrations. Fossil assemblages can differ in their taxonomic diversity (from monotaxic to polytaxic), taphonomic signatures and sedimentologic fabric. The origin of these assemblages can be related by a complex interplay of both intrinsic and extrinsic factors. The intrinsic factors are mainly associated both morphology and ecology of the organisms. Constructional morphology aspects, such as the body design, skeletal construction, type of skeletal material and connective tissue, influence post-mortem history and consequently the preservation potential. The features of the fossil assemblage are even related to the ecology and ethology of organisms, such as pelagic or benthic lifestyle, substrate relationship (epifaunal and infaunal habits) as well as gregarious behaviour and reproductive aggregations. As regards the extrinsic factors the characteristic of these assemblages are linked to physical and chemical environmental parameters, as well as the tectono-sedimentary context which influence for example, the rate of sedimentation.

The focus of the present work is to decipher the taphonomy and sedimentology of some oligospecific high dense fossil assemblages of well-preserved, multi-element skeleton invertebrates, such as arthropods and echinoids. The purpose of the dissertation is to shed light on the origin and palaeoecology of the fossil accumulations and, through the study of very dissimilar organisms, such as arthropods and echinoids, which pertain to different phyla and show different mode of life, to explain the nature and the distribution of the fossil concentrations across a wide spectrum of environments.

Why to study arthropods and echinoids?

Four main aspects promote the study of fossil arthropods and echinoderms from Sardinia:

1) Fossil arthropods and echinoderms of Sardinia have been subject to various systematic studies as early as the second half of the 19th century, while contributions on their taphonomy, sedimentology and palaeoecology sporadically were made.
2) Both arthropods and echinoderms show an extensive fossil record and can form dense accumulations.
3) Currently these invertebrates are common members of the marine communities. Field and laboratory observations on the ecology and taphonomy of these organisms, through an actuopalaeontological approach, can enable direct correlations between living and fossil communities and permit to infer the processes from which well-preserved fossil accumulations originated.
4) Arthropods and echinoderms are multi-element skeletons invertebrates which tend rapidly to disarticulate under normal marine conditions. The exquisite preservation of complete articulated skeletons requires exceptional environmental conditions of deposition; therefore these organisms can be, potentially, good indicators of taphonomic processes and provide important insights into depositional dynamics.

General methods

The dissertation is divided into two parts:

The first part is focused on the fossiliferous beds of Riu Is Arrus Member, Monte Argentu Formation (Upper Ordovician), where a dense accumulation of the soft-bodied arthropod *Tariccoia arrusensis* was found.

The second part is mainly focused on several regular and irregular echinoid mass occurrences from the Early to Middle Miocene of Sardinia.

The cases studied exhibit exceptional concentration or conservation of fossil remains.

The palaeoecologic and genetic interpretation of fossil concentrations required three-phase procedure:

1) Analysis of the composition, diversity and abundance within the fossil assemblages.
2) Taphonomic characterization of the constituent fossil assemblage to reconstruct shell histories both before and during the formation of concentrations. Taphonomic signatures include preservation state, disarticulation, fragmentation, abrasion, encrustation and orientation of fossil material relative to the bedding in both plan and cross section.
3) Stratigraphic and sedimentological characterization of the shell rich sedimentary body to identify the most likely late-stage processes of concentrations. Moving from smaller to larger scale, three levels are analyzed: Microfacies analysis, stratinomic analysis and facies analysis.

Therefore, a taphonomic, sedimentologic, stratigraphic and ecologic integrated approach is require to infer, at high level of confidence, the genesis of the arthropod and echinoid assemblages.

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PART I

ARTHROPODS

Chapter 1.

General overview on the Palaeozoic arthropod fauna of Sardinia

1.1. Previous studies on the Palaeozoic arthropods of Sardinia

The Palaeozoic sediments of the South-western Sardinia, particularly the Cambrian and Ordovician deposits, contain a rich and diversified arthropod fauna, which has been subjected to various studies as early as the second half of the 19th century. The first reference was provided by Meneghini (in Lamarmora, 1858), who described trilobites from the Upper Ordovician Portixeddu Formation. Cambrian trilobite faunas were studied by Meneghini (1881, 1885, 1888) and Bornemann (1882) who described the *Dolerolenus*-dominated fauna of the Canal Grande area. Further studies were conducted by Gambera (1897) and Pompecky (1901) who described the *Paradoxides* fauna of the Cabitza shale.

In the second half part of the 20th century a revision of the Cambrian trilobite fauna was provided by Rasetti (1972). More recent studies (Pillola, 1986, 1990a, 1990b, 1991a, 1991b; Loi et al., 1995, 1996; Alvaro et al., 2003; Elicki and Pillola, 2004; Dies Alvarez et al., 2010) contributed to clarify trilobite systematic, biostratigraphy and sedimentology of the Lower to Middle Cambrian succession of the Sulcis-Iglesiente area. An important contribution to the study of trilobite taxonomy, with the description of 86 species belonging to 57 genera, and lithostratigraphy of the Upper Ordovician sequence of the southwest of Sardinia was provided by Hammann and Leone (1997, 2007).

1.2. Geology and palaeogeography of South-western Sardinia in the Early Paleozoic

During the Cambrian and Ordovician Sardinia was located along the north margin of the Gondwana Continent and was involved into the future (Late Palaeozoic) Variscan mountain chain (Stampli and Borel, 2002; Von Raumer et al., 2003) (Fig. 1). The Palaeozoic basement of Sardinia represents a complete section of Variscan orogen (chain), which detached and drifted towards Southwest, from the Southern Europe, during the Oligo-Early Miocene (Carmignani et al., 1989). As discussed by Carmignani et al., (1989), this Variscan basement consists of a metamorphic high grade complex (Northern Sardinia), a nappe zones verging to SW and an autochthonous external zone (South-western Sardinia), affected by thrust and folds (Fig.2). In the external zone (Sulcis-Iglesiente area) a thick Cambrian to Ordovician sedimentary sequence, related to the development of a continental platform (shelf), extensively crop outs.

The Lower Paleozoic sedimentary rocks of the Sulcis-Iglesiente area belong either to autochthonous and parautochthonous/allochthonous structural units. The autochthonous succession consists of two main sequences, which are separated by an angular unconformity, related to the compressive movements of the "Sardic Phase" (Stille, 1939), whose age lies between the Tremadocian and Caradocian (Leone et al., 1991).

The lower sequence, which consists of a Early Cambrian to Tremadoc deposits, forms a thick succession of about 2000 – 2500 metres. This sequence has formerly been distingushed into three major lithological units (Pillola, 1990, 1991a): a basal terrigenous succession with carbonatic intercalations (Nebida Group), a middle portion consisting entirely of carbonate rocks (Gonnesa Group), and a mainly terrigenous upper unit (Iglesias Group), the uppermost of which has been regarded as Tremadocian on the basis *Rhabdinopora flabelliformis* and acritarchs (Barca et al., 1987; Pillola and Gutierrez-Marco, 1988; Pillola et al., 2008).

The post-Sardic, sequence which starts with “Puddinga” sediments (Monte Argentu Formation) and ends, without any apparent disconformity, with Early Silurian rocks, is represented by five formations and nine members whose stratigraphic relations and sedimentological features were described by Leone et al. (1991) and Laske et al. (1994) (Fig.3). More sedimentological and environmental data of this Middle to Upper Ordovician sequence, which shows a wide range of both continental, transitional and marine facies, have been reported by Leone et al. (1995) and Leone et al. (2002).

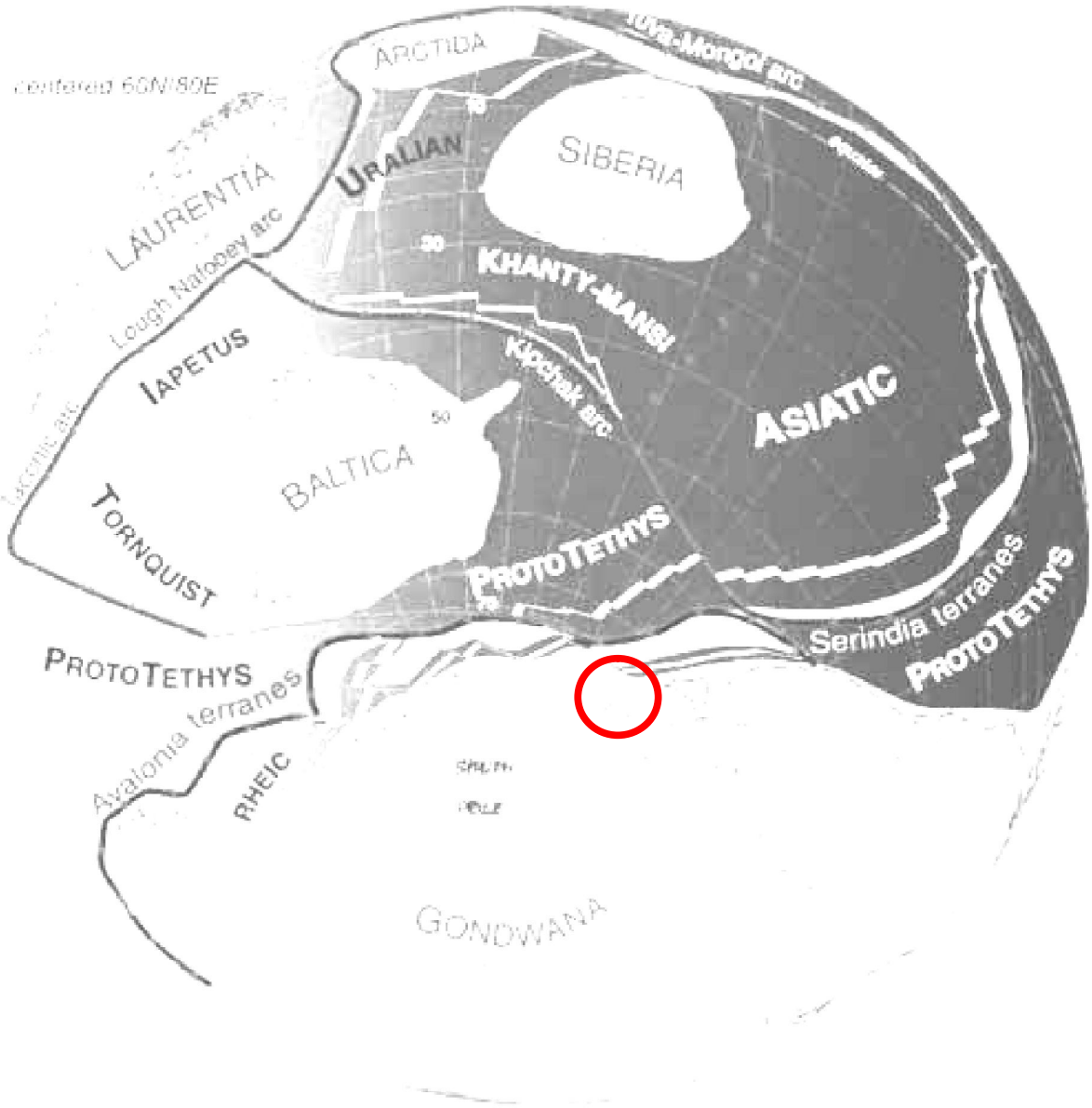

Figure 1. Plate-tectonic situation for the Early Ordovician (Tremadocian) (490 Ma), from Stampli and Borel (2002). Red circle indicates the position of Sardinia at the north margin of Gondwana.

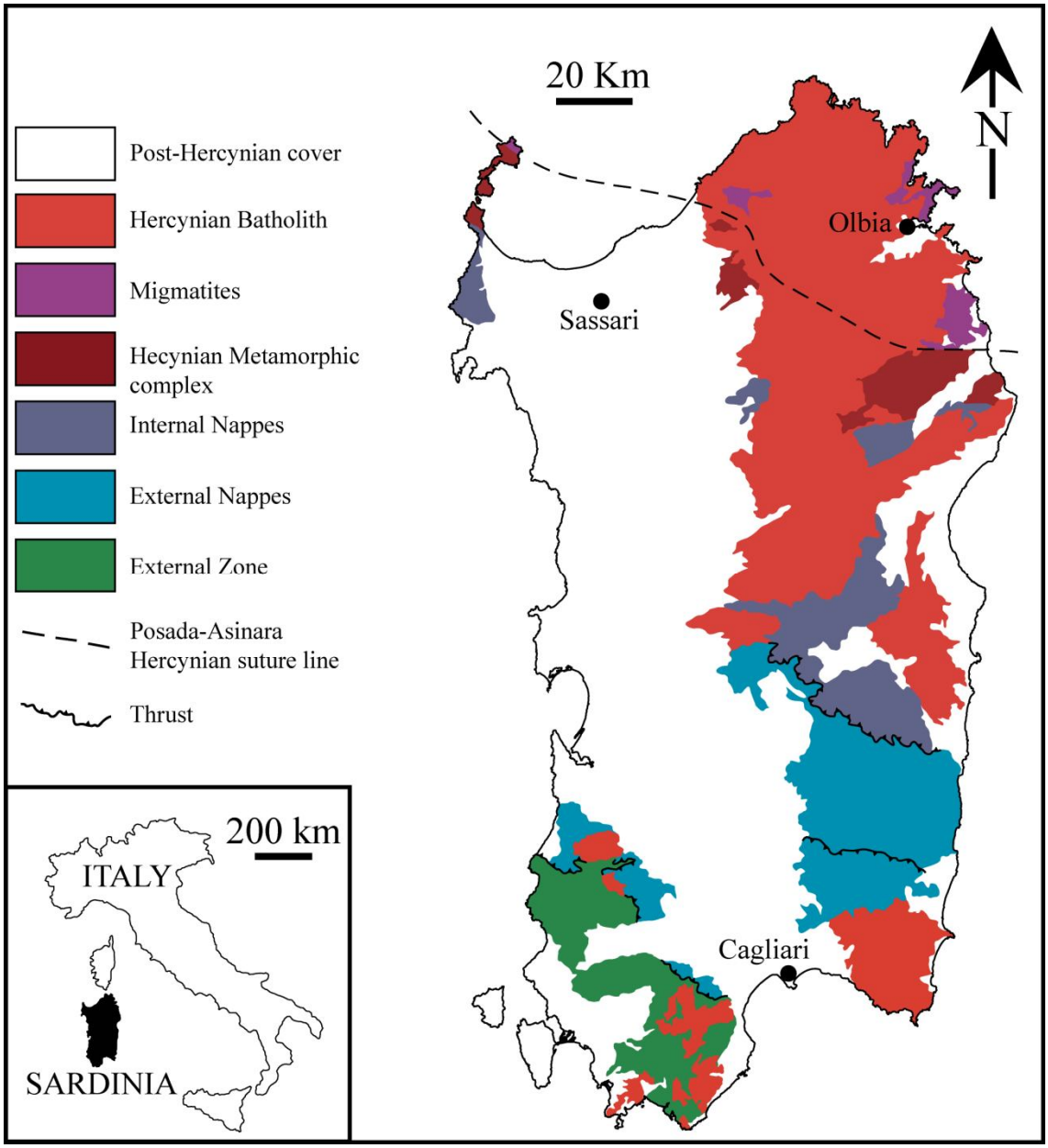

Figure 2. Tectonic sketch map of the Hercynian basement of Sardinia, (After Carmignani et al., 1989 and 2001, simplified).

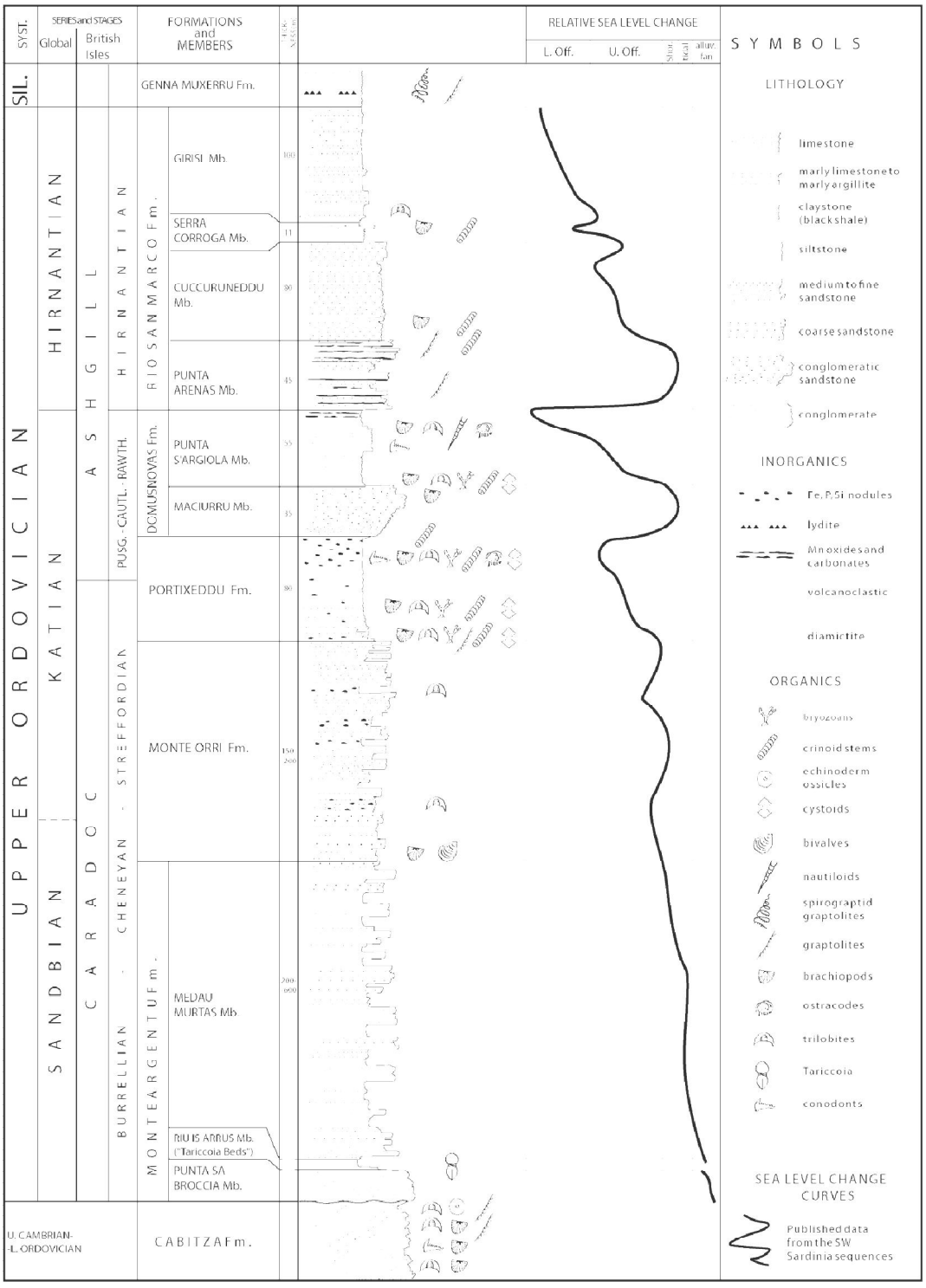

Figure 3. Post-Sardic Ordovician sequence of SW Sardinia (from Leone et al., 2002).

Chapter 2.

The turbulent path of *Tariccoia arrusensis*: taphonomy and palaeoecology of an Ordovician nektaspid endemic to Sardinia

Within the massive grey siltstones of the Riu Is Arrus Member (Laske at al., 1994), Monte Argentu Formation, which is cropping out widely along the valley of the creek Riu Is Arrus, SE Fluminimaggiore (SW Sardinia), a rich deposits of the trilobite-like arthropod *Tariccoia arrusensis* were found.

In order to shed light on the palaeocology of this peculiar arthropod stratigraphic, sedimentologic and taphonomic studies of two stratigraphic section of Riu Is Arrus Member were made.

The main goals of this study are:

- To document the stratigraphy and sedimentology of Riu Is Arrus Member.
- To investigate the taphonomy of *Tariccoia.*
- To propose a detailed palaeoenvironment and palaeoecology reconstruction.

2.1. Morphology and systematic position of *Tariccoia arrusensis*

Tariccoia arrusensis Hammann et al. (1990) is an Upper Ordovician trilobite-like arthropod endemic to Sardinia.

This arthropod has a non-mineralized, presumably chitinous, smooth exoskeleton, without abaxial trilobation (Fig. 4). The Cephalon, which is devoid of eyes, is strongly vaulted with anterior and lateral margins rounded and passing continuously into a ventral doublure. The trunk is narrower than cephalon and consists of four smooth tergites with rounded lateral tips. The pygidium, which has a sub-triangular scutcheon-like outline, carries a median longitudinal crest and shows a broad ventral doublure.

T. arrusensis has been described for the first time by Hamman et al. (1990), who rejected the classification of Taricco G. (1922), that assigned the incomplete remains of *Tariccoia* to different genera of phyllocarids such *Ceratiocaris, Caryocaris* and *Lingulocaris.* The systematic classification of the Genus *Tariccoia* is uncertain due to the fact that no appendages are preserved; Hammann et al. (1990) and Hammann and Leone (1997) argue that *Tariccoia* most closely related to the Polish Cambrian genus *Liwia* Dzick and Lendzion 1988 and therefore a member of the family Liwiidae Dzick and Lendzion 1988 included in the Order Nektaspida.

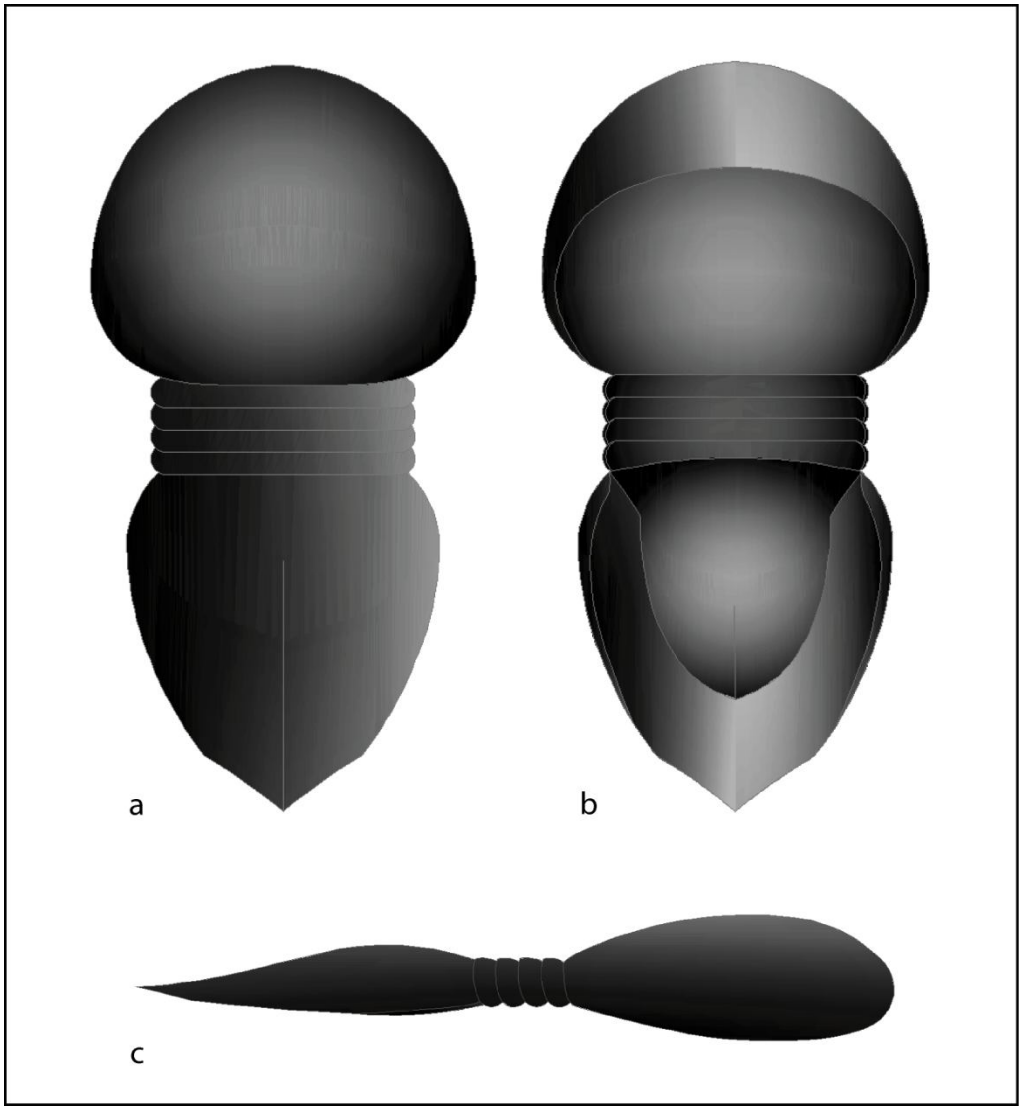

Figure 4. External morphology of *Tariccoia arrusensis* (Hammann et al., 1990). a) dorsal view; b) ventral view; c) lateral view.

2.2. Material and Methods

The excellent outcrops of Riu Is Arrus Member allowed intense sedimentological, palaeontological and taphonomical field and laboratory studies. A detailed facies analysis has been carried out through a study of the lithological, sedimentological, palaeontological and taphonomical features, determined during the logging of two stratigraphic sections at the 1 / 40 scale. The lithological and sedimentological study consists of mineralogical-petrographic analysis in thin section and the observation of the sedimentary structures on the cut slabs; mineral phases of grey siltstones of Riu Is Arrus Member was evaluated using X-ray diffraction (XRD).

For the X-ray diffraction analysis, samples were lightly ground in an agate mortar, and ~200 mg of the powder of each sample were packed into the sample holder. XRD analysis was performed using conventional θ-2θ equipment (Panalytical) with CuK_{α} wavelength radiation (λ = 1.54060 Å), operating at 40 kV and 40 mA, using the X'Celerator detector.

The taphonomic investigation, which will be exhaustively discussed below, covered both stratigraphic sections and in particular an area of 65 m^2 and a thickness of 50 cm in between meters 17 and 18 of the Roia Srappas section. The attributes selected to characterized the taphonomy of *Tariccoia* include preservational mode, sorting, bioclastic accumulation, fragmentation, alignment, dorsoventral orientation. These taphonomic attributes were recorded for 110 remains of *Tariccoia* preserved in situ.

More than one hundred samples of *Tariccoia arrusensis* fossil were collected systematically along the entire sections measured. Some specimens required mechanical prepraration with a pneumatic airscribe to expose the fossil remains. The specimens of *T. arrusensis* used in this study are housed in the Department of Earth Sciences, Cagliari, Sardinia.

2.3. Geological setting and local stratigraphy

In the Sulcis-Iglesiente area, the post-Sardic Phase Ordovician autochthonous sequence starts with the Monte Argentu Formation (Laske et al., 1994) which unconformably covers the sediments of the middle Cambrian to Tremadocian Cabitza Formation (Pillola and Gutierrez Marco, 1988) (Fig. 5A). The Monte Argentu Fm., the so-called «Puddinga» by local geologists (Units a1-a3, Hammann et al., 1990; Puddinga sequence, Leone et al., 1991) is a terrigenous succession, subdivided, from base to top, into three members, the Punta Sa Broccia Member, the Riu Is Arrus Member and the Medau Murtas Member (Laske et al., 1994). In outcrops of the Rius Is Arrus area (SE of Fluminimaggiore), (Fig. 5B) the Punta Sa Broccia Member consists largely of red-purple conglomerates interbedded with siltstone and sandstone; this member forms a fining upward succession that often is made of 2-3 individual sequences (Martini et al., 1991; Laske et al., 1994). The lithologies that characterize the upper part of the Punta Sa Broccia Member consists mostly of medium to fine grain gravel, with a red-coloured matrix of sand and silt, passing upward to gray-green conglomerates. The conglomerates are massive, predominantly clast-supported although rich in matrix; the clasts appear from sub-angular to sub-rounded and are composed of slate, sandy slate, limestone, quarzitic sandstone, quartz single crystal and polycrystalline, coming mainly from Iglesias and Gonnesa Groups. With the exception of rare horizontal traces no fossils have been found up to now. The Punta Sa Broccia Member is covered by the Riu is Arrus Member, mainly characterized by grey fossiliferous siltstones with intercalations of sandstone and microconglomerate. The microconglomerates in the medium to lower Riu Is Arrus Member are generally clast-supported with massive or normal graded stratification and consisting mainly of lithic fragments of shale and sandstone and medium-fine polycrystalline quartz and rare feldspar. The grey siltstones

that characterize the Riu Is Arrus Member usually lack sedimentary structures and show a complete lithological homogeneity. The member can not be found only in the Fluminimaggiore area but also in the areas near Domusnovas and Gonnesa-Bacu Abis. The Medau Murtas Member consists of red-purple to green siltstone with interbedded sandstone and conglomerate of the same composition as those of the Punta Sa Broccia Member with the exception of undetermined trace fossils of *Skolithos*-type, no fossils have been found. The palaeoenvironmental interpretation of the Punta Sa Broccia Member deposits were subject of dispute; they are currently considered as overlapping alluvial fans (Martini et al., 1991; Laske et al., 1994). The siltstone and sandstone at the top of the formation, related to Medau Murtas Member, are interpreted as low relief areas, probably coastal floodplains crossed by river channels with local marine influence in the upper part of the member (Martini et al., 1991; Laske et al., 1994). The grey sediments of the Riu Is Arrus Member form a distinct horizon between the two members; the depositional environment of this member is still matter of debate: Hammann et al. (1990) supposed a sheltered bay with restricted marine conditions. The Monte Argentu Formationis covered by Monte Orri Formation which in the Fluminimaggiore area consists of a siliciclastic succession 100 meter thickness. This formation shows the first undoubtedly marine fossils of the post-Sardic sequence. The fauna show a low-diversity and is largely dominated by trilobites, especially *Deanaspis* and *Dalmanitina.* A fossiliferous outcrop with a graptolite assemblage of Caradocian age has been discovered near Fluminimaggiore (Leone et al., 1993). This level could be stratigraphically assigned to the uppermost part of the Monte Orri Formation.

Fine sandstone, siltstone and claystone characterize the Portixeddu Formation that overlies the Monte Orri Formation. The Portixeddu Formation shows a rich fauna containing prevalent brachiopods, bryozoans and echinoderms and subordinately

trilobites, bivalves, cephalopods, ostracods, graptolites etc. The fauna is generally accumulated in tempestites or condensed levels of an offshore environment.

2.4. Stratigraphy and sedimentology

Along the Riu Is Arrus valley, SE of Fluminimaggiore, two complete stratigraphic sections of the Riu Is Arrus Member are measured near the old building Sa Palazzina (N39°25'35''– E8°30'35'') and in the area Roia Srappas (N39°25'14''– E8°32'36''), which are located about 3.5 km from each other (Fig. 5B). The thickness of the Riu Is Arrus Member varies considerably in the two studied sections. In the locality Roias Srappas the Riu Is Arrus Member has a thickness of about 45 meters which is reduced to about 29 meters in the Sa Palazzina section (Figs. 6A, B and 7).

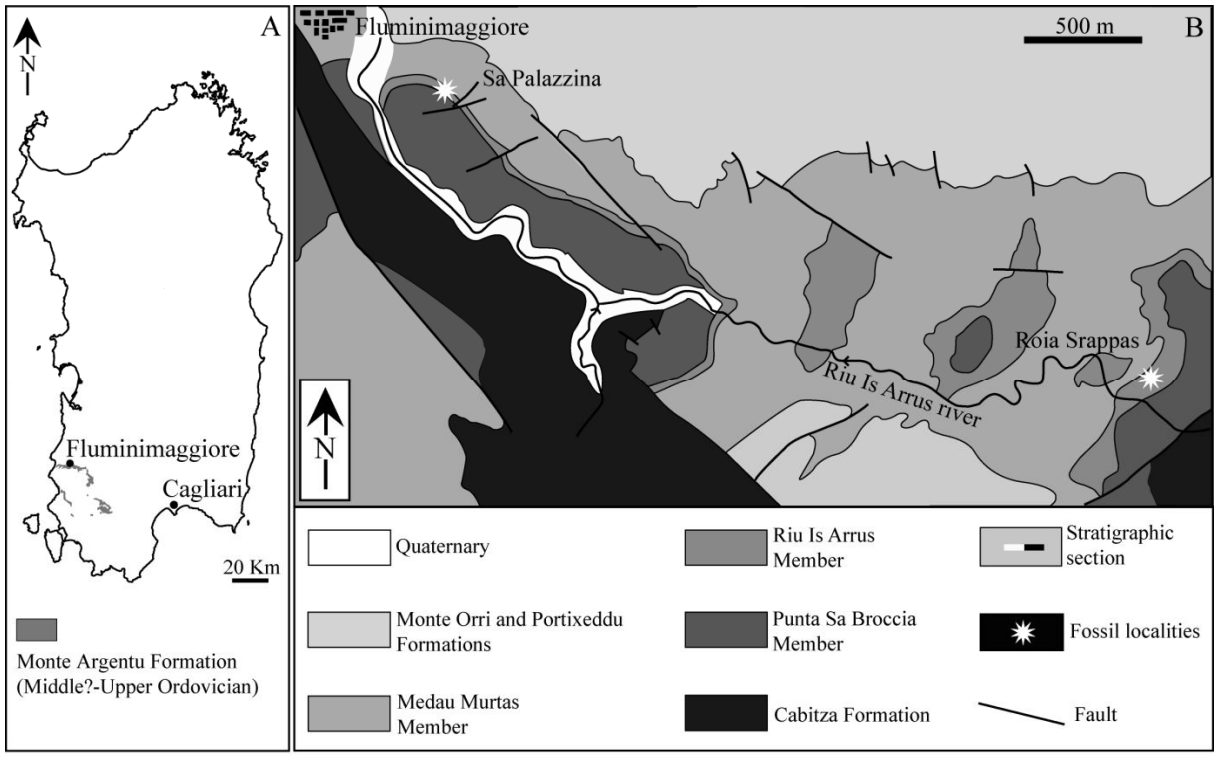

Figure 5. A) Outcrop distribution of Monte Argentu Formationin the Sulcis-Iglesiente area, SW Sardinia. B) Simplified geological map of the area around the village of Fluminimaggiore. The asterisks indicate Sa Palazzina and Roia Srappas stratigraphic sections, (after Gartiser (1990) and Hammann and Leone (1997), modified).

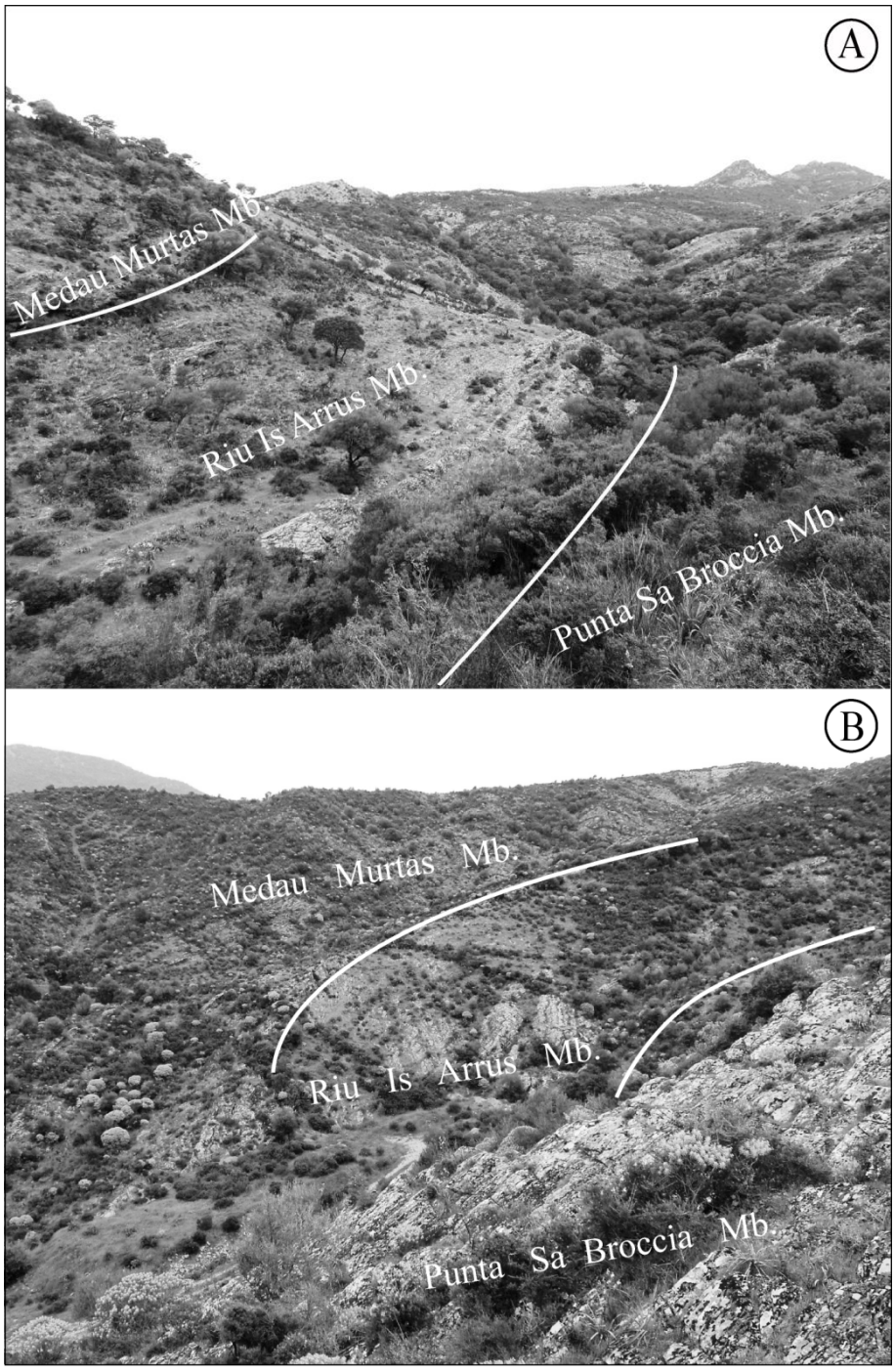

Figure 6. Panoramic view of the two measured stratigraphic sections of the Monte Argentu Formation: A) Roia Srappas section; B) Sa Palazzina section.

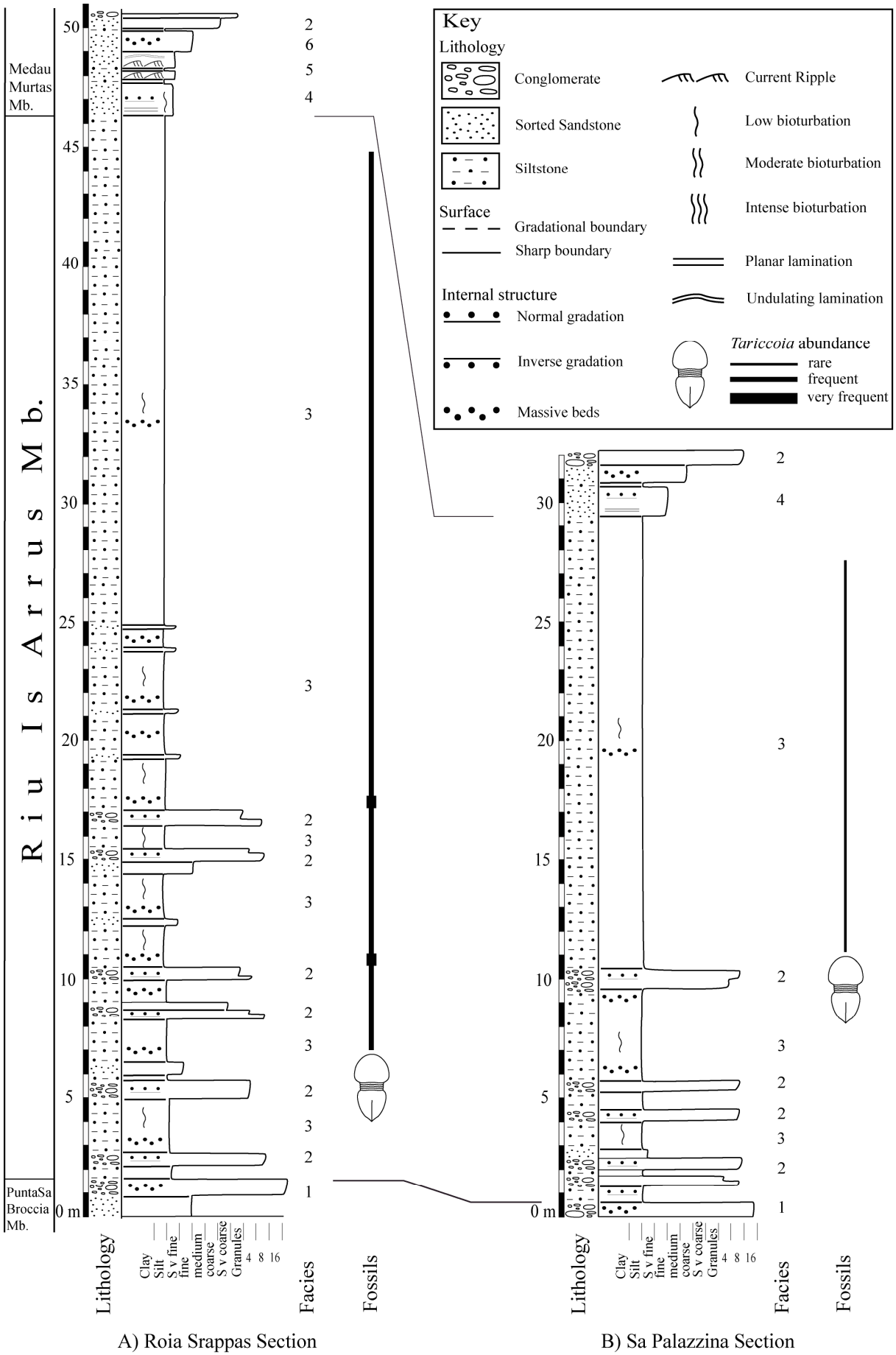

Figure 7. Stratigraphic sections of Riu Is Arrus Member at A) Roia Srappas and B) Sa Palazzina localities.

2.4.1. Facies analysis

In the studied stratigraphic sections, six sedimentary facies were recognized on the basis of their lithology, sedimentary structures and fossils remains:

Facies 1 consists of red to purple polymictic conglomerates that alternate with purple-green siltstones and fine sandstone. The conglomerates are massive or subordinately normally graded. The lithic clasts range from sub-rounded to rounded and consist of sandstones and siltstone with size ranging from 2 mm to 10 mm. The quartz pebbles are sub-angular with a size of about 3 mm. These conglomerates are predominantly clast-supported and the matrix usually consists of fine sand and silt. The purple-green siltstone beds have a thickness of 0.5 to 2m and are massive or laminated. Beds contacts are planar or slightly wavy, and rarely erosive.

Facies 2 is made up of massive greenish-grey polymictic microconglomerates interbedded with massive or crudely stratified sandstones (Figs. 8A and B). The beds, which are 30 to 50 cm thick, often result from the overlapping of a distinct fining-upward sequence. The clasts of the poorly sorted conglomerates are sub-angular to sub-rounded, with maximum size of 8 mm and consist predominantly of lithic fragments (quartz, feldspar, sandstone and siltstones). These conglomerates are predominantly clast-supported with sandstone matrix. The coarse-medium grained sandstones show some distinct levels with small (from 1 to 5 mm) aligned pebbles. Lower and upper bed contacts between the two lithologies are sharp and planar.

Facies 3 consists of grey siltstones which commonly appear massive and featureless with rarely laminated intervals (Figs. 8C, D and E); sporadic fine sandstones levels occur. As for the mineralogical composition, the siltstones consist of sub-angular to sub-rounded quartz grains, with maximum size of 90 μm, and clay minerals; X-ray

diffraction indicates the presence of Chlorite (Clinochlore) and Illite (Fig. 9). The laminated beds are normal graded and alternately rich in quartz grains or clay minerals. The sporadic presence of distinct burrows, the uneven distribution of the quartz grains and interruption of the primary bedding in the laminated beds provide evidence of bioturbation. The siltstones contain an oligotypic taphocoenosis characterized by *Tariccoia arrusensis* and presumably algal remains.

Facies 4 consists of 1.5 m-thick parallel laminated green sandstone interbedded of brown mudstone. Sands beds are usually 0.3-1 cm thick, and alternate with 0.2-1 cm of mudstone. The stratification is disrupted by vertical burrows, (ichnofabric index 3). The green sandstones are normal graded and are made up of lithics and quartz grains from sub-angular to sub-rounded.

Facies 5 is characterized by alternantion of poorly-sorted fine to medium grained sandstones and medium siltstones (Figs. 10A and B). Beds show massive to flat-undulating lamination. There are coarsening and fining upward beds and distinct intervals with uni-directional current ripples and climbing ripples. These ripples have a wavelength of 18 cm and height of 2 cm and show a strong clay fraction in the leeside laminae. Sometimes the ripples, while preserving the surface, are draped by grey siltstone which is about centimetre thick. The siltstones are commonly massive and show low bioturbation such *Planolites*-type and syneresis cracks. Frequently the contacts between the ripple beds and the underlying siltstone are erosive.

Facies 6 is characterized by massive sandstones with normal/inverse grading sequence with massive grey siltstones interbedded (Figs. 11A andB). The medium sandstones range from a few decimetres to a meter thick with 2 to 10 cm thick siltstones interbedded. The sandstone clasts are from sub-angular to sub-rounded with size from 0.2 to 1 mm. The mineralogical composition of the clasts is dominated by quartz and

lithics with subordinately small clay or silt chips. The sandstone/siltstone bed contacts are sharp and planar.

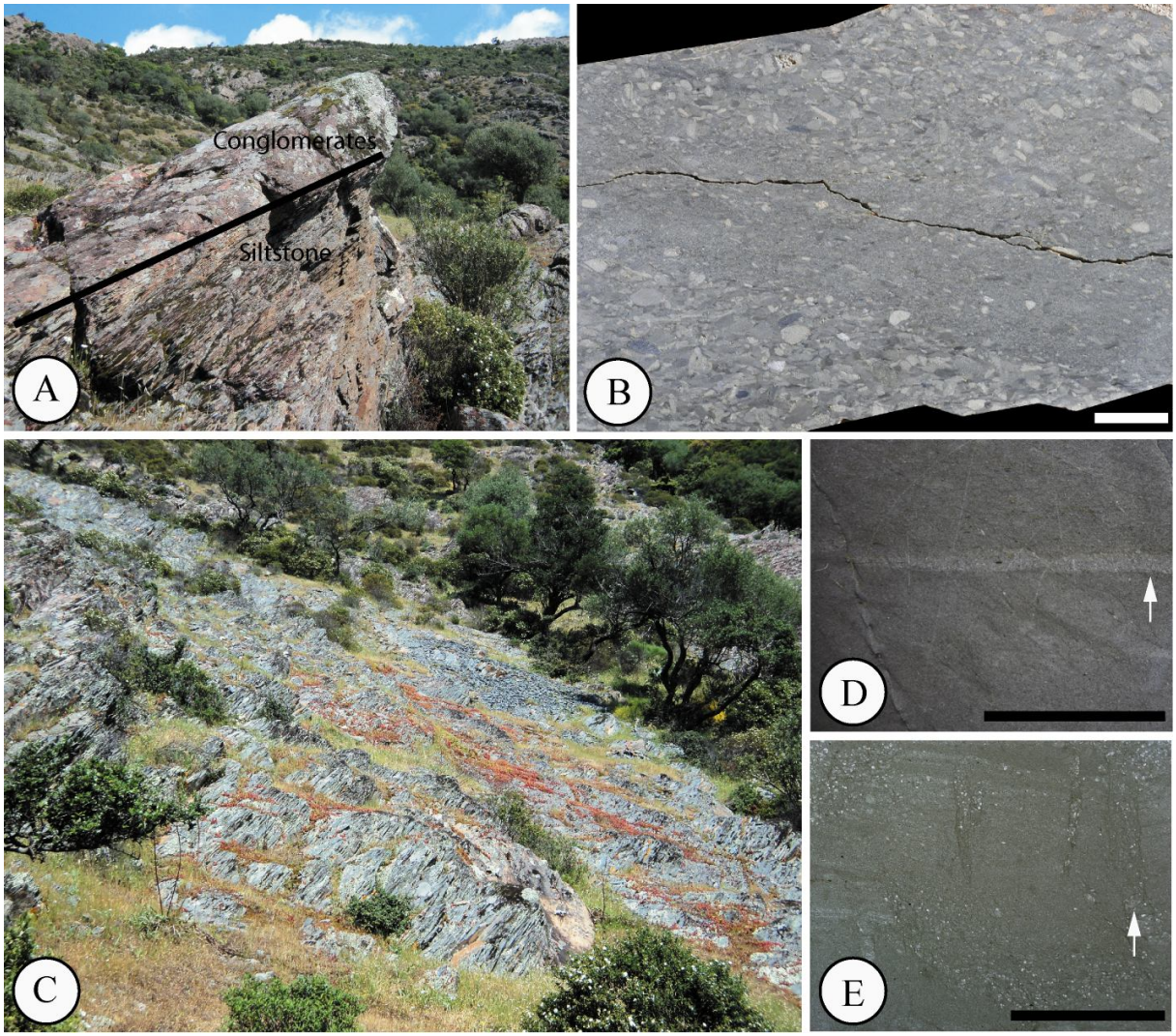

Figure 8. Roias Srappas: A) Conglomerate/siltstone alternations in the lower part of the section; B) Polished slab of the conglomeratic levels (facies 2); C) Field view of grey siltstone levels where *Taricciola* remains were found (facies 3); D) Thin section of grey siltstones showing massive aspect; E) Thin section of grey siltstone showing intense bioturbation and vertical burrows (see white arrows); Scale bars represent 1 cm.

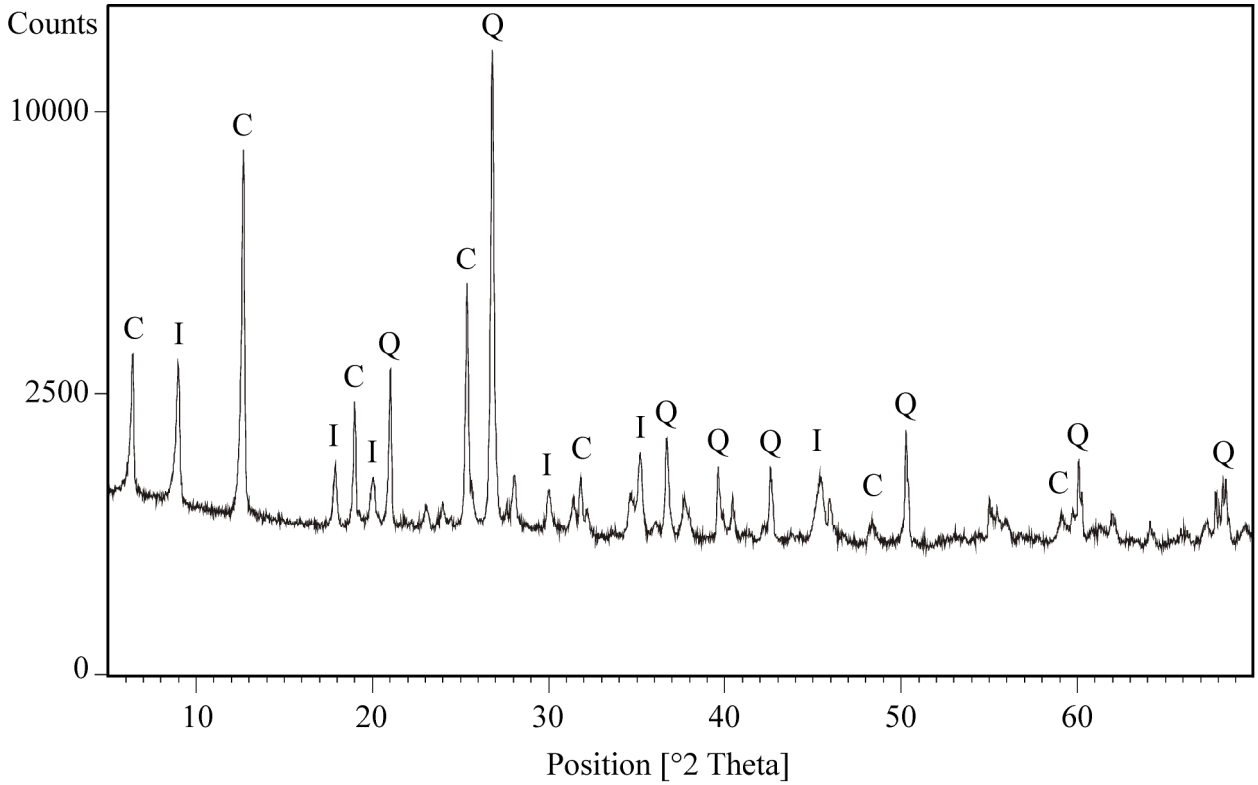

Figure 9. X ray diffraction analysis of the grey siltstones (facies 3). C Clinochlore; I Illite; Q quartz.

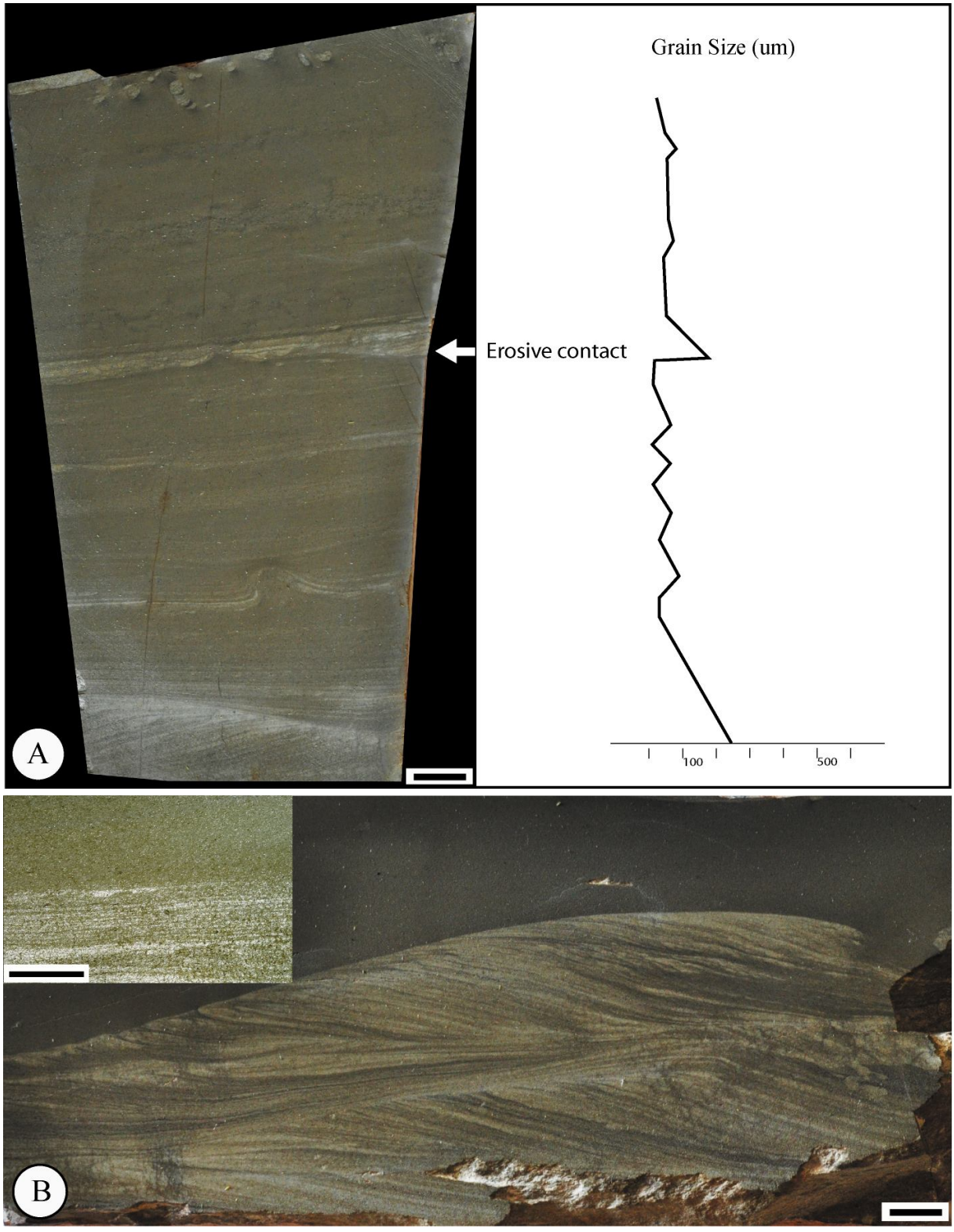

Figure 10. A) Alternations of fine to medium grained sandstones and medium siltstones (facies 5); this facies shows massive to flat-undulating lamination and current ripples. Scale bar = 1 cm. B) Current ripples draped by massive grey siltstones (facies 5). Scale bar represents 1 cm.

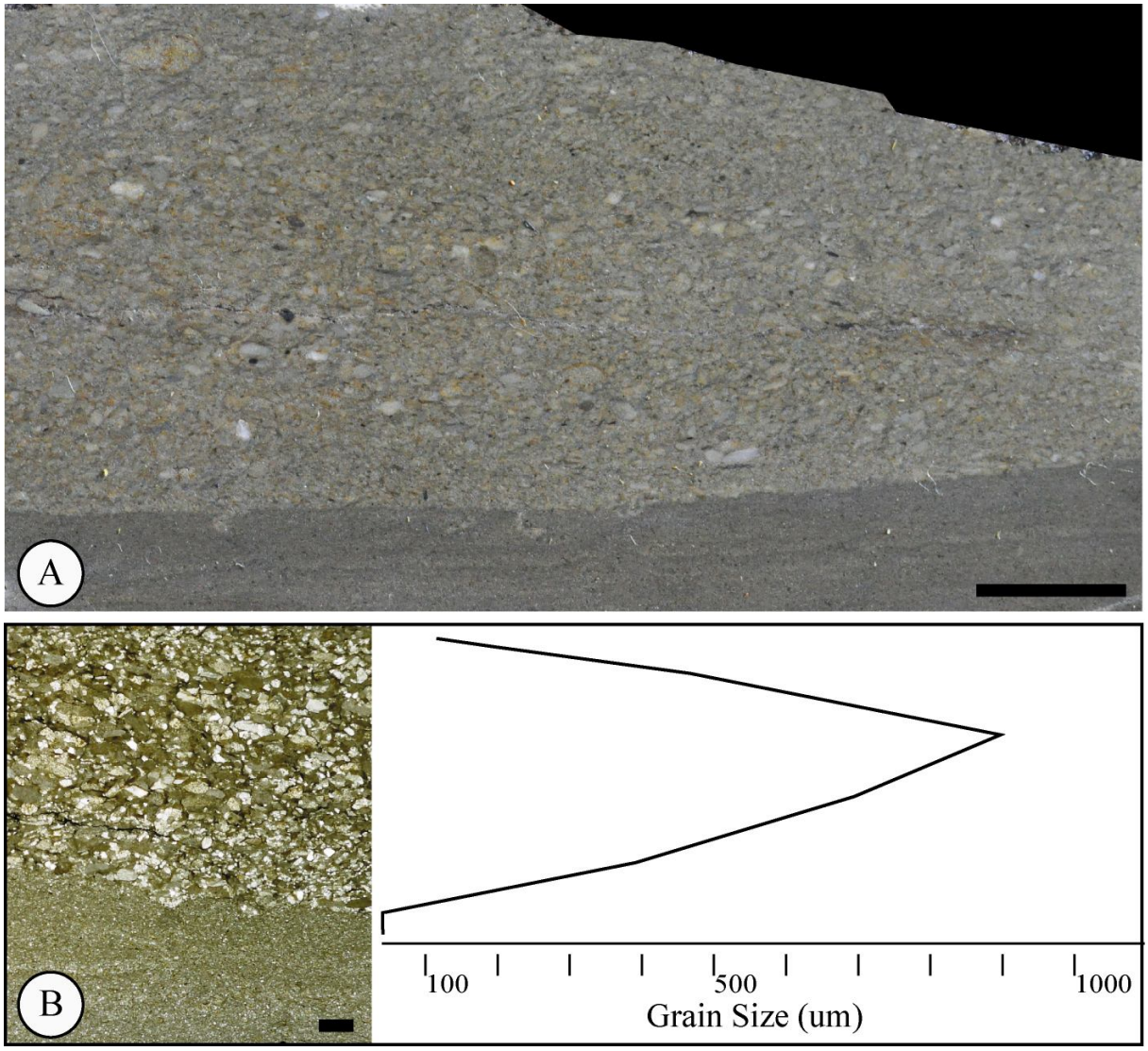

Figure 11. A) Coarse massive sandstones with massive grey siltstones interbedded (facies 6). Scale bar represents 1cm. B) Massive sandstones showing normal/inverse grading (coarsening-fining upward) mm-sequence, (facies F). Scale bar represents 1mm.

2.5. Taphonomy

The two sections greatly differ for the fossil content. In the Palazzina section the *Tariccoia* remains are rare and usually disarticulated while the locality Roias Srappas shows a great number of well preserved arthropods. In the Roias Srappas section the arthropod remains are found from the seventh meter of the section measured and reached a very high density in the first decimetres above the microconglomerate layers. A large number of complete and disarticulated remains of *Tariccoia* were counted *in situ* and biostratinomically evaluated. Particularly the counting has covered an area of 65 m^2 and a thickness of 40 cm between meters 17 and 18 of section (Fig. 12A).

Preservation: The exoskeleton of *T. arrusensis*, is preserved as a thin carbonaceous film, the altered form of presumably chitinous cuticle; occasionally the exoskeletons are limonitised. Sporadic pyrite crystals occur on the ventral side of the arthropods. Although all remains of *T. arrusensis* show a three-dimensional preservation there are specimens that show compression. Compression is evident by the wrinkling of the dorsal exoskeletons, which is usually due to sediment compaction.

Relative abundance of sclerites: Of the 110 sclerites counted, 45% of the specimens are complete, 17% are pygidium, 36% are cephalons and 2% are thoracopygida (Fig. 14A).

Accumulation: The distribution of sclerites of *Tariccoia* throughout the section is non-uniform. The remains are both randomly distributed within the siltstones and accumulated in high density on discrete bedding plane.

Disarticulation and breakage (fragmentation): *T. arrusensis* is preserved in various states of disarticulation, both articulated exoskeletons or in a state of incipient disarticulation and isolated cephalons and pygidia (Fig. 13A, B and C). The articulated specimens show two or three segments of the thorax as the first segment is always

covered by the cephalon. Articulated specimens are always devoid of appendages. The exoskeleton elements of *Tariccoia* rarely are broken; only one pygidium shows evidence of breakage**.**

Size and Sorting: Usually the specimens are deformed by tectonic strain and consolidation (compaction), therefore exact biometric data could not be achieved. The total length of the weakly deformed specimens ranges from 1 to 5 cm (Fig. 9). Complete specimens and disarticulated cephalons and pygidia of different size are present on some bedding plane. Isolated anterior and posterior shields, which are found close to each other on the same bedding plane, are often comparable in size and might be parts of a single specimen.

Preferred orientation in plan view: Both the complete exoskeletons and sclerites of *Tariccoia* do not show preferred orientation in plain view. The long axes of articulated exoskeletons and sclerites are randomly orientated (Fig. 13C).

Dorsoventral orientation: all remains are concordant or subconcordant to the bedding; isolated cephalons and pygidia show a feeble preference for a convex-down orientation while about 95% of articulated specimens are imbedded with the convex dorsal side down or oblique down (Figs. 14B, C and D; 12B and C).

Taphofacies: On the basis of the biostratinomic parameters described above the siltstones of Riu Is Arrus Member are characterized by two taphofacies named Tf1 and Tf2

Tf 1: this taphofacies consists of high density of exoskeletons in different stages of disarticulation. Detailed observations reveal a predominance of articulated remains (45% of total remains) with preferred convex down orientation (Fig. 13C).

Tf 2: the taphofacies is characterized exclusively by the accumulation of disarticulated sclerites. The sclerites do not show sorting and preferred orientation and there is no evidence for abrasion or fragmentation**.**

Figure 12. A) Field photographs of the grey siltstone levels from which the arthropod biostratinomic data presented herein were collected. Counting was carried out in an area of 65 m^2 and a thickness of 50 cm. *Tariccoia* remains were found both convex down (B) and convex up (C) oriented. Scale bars represents 1 cm.

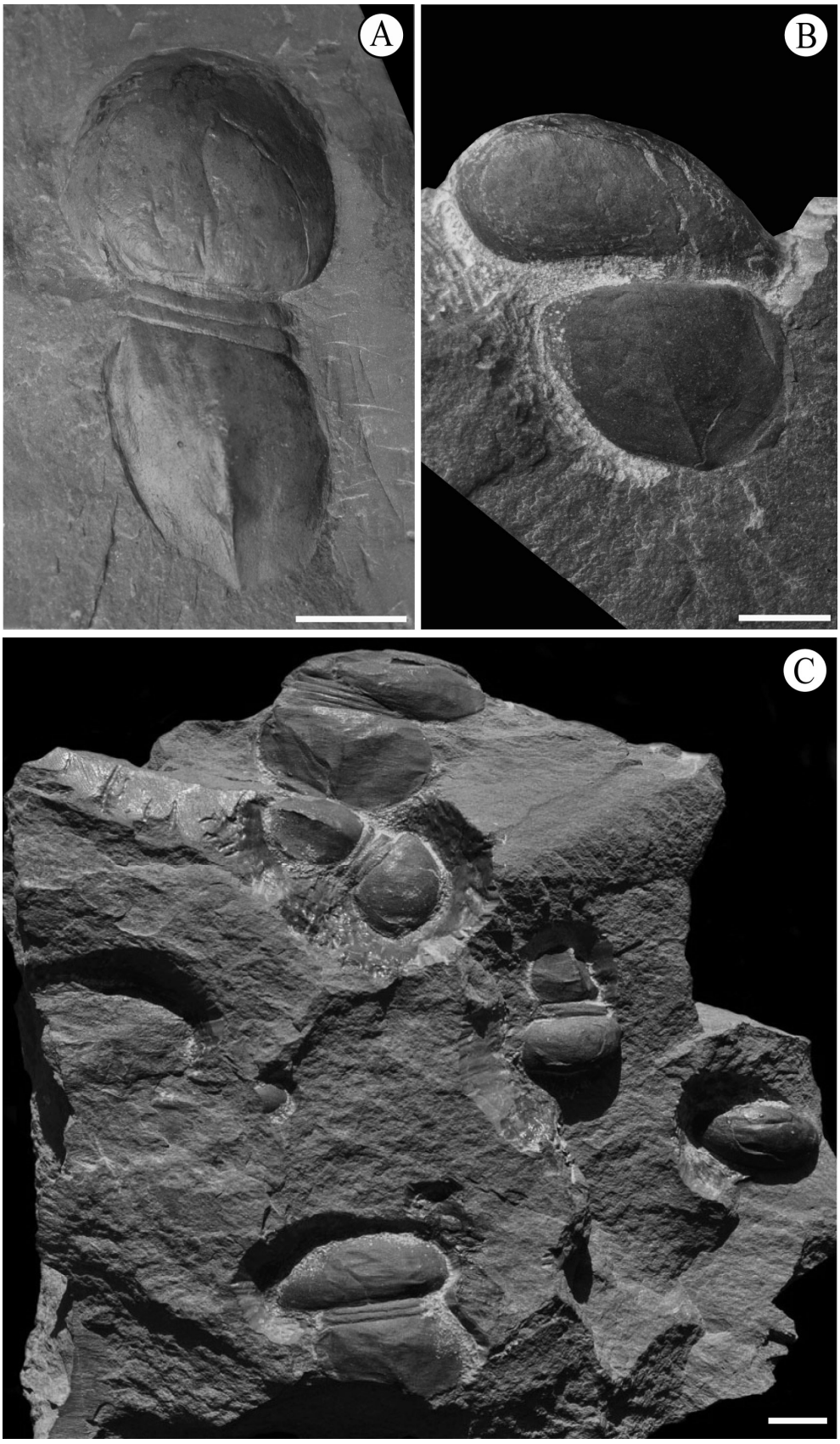

Figure 13. *Tariccoia arrusensis*: A) Complete exoskeleton showing two thoracic segments (DSTCP23193); B) Specimen lacking of the thoracic segments (DSTCP23192a); C) Dense accumulation of complete exoskeletons showing the same dorsoventral orientation (PAS8053). Scale bars represents 1cm.

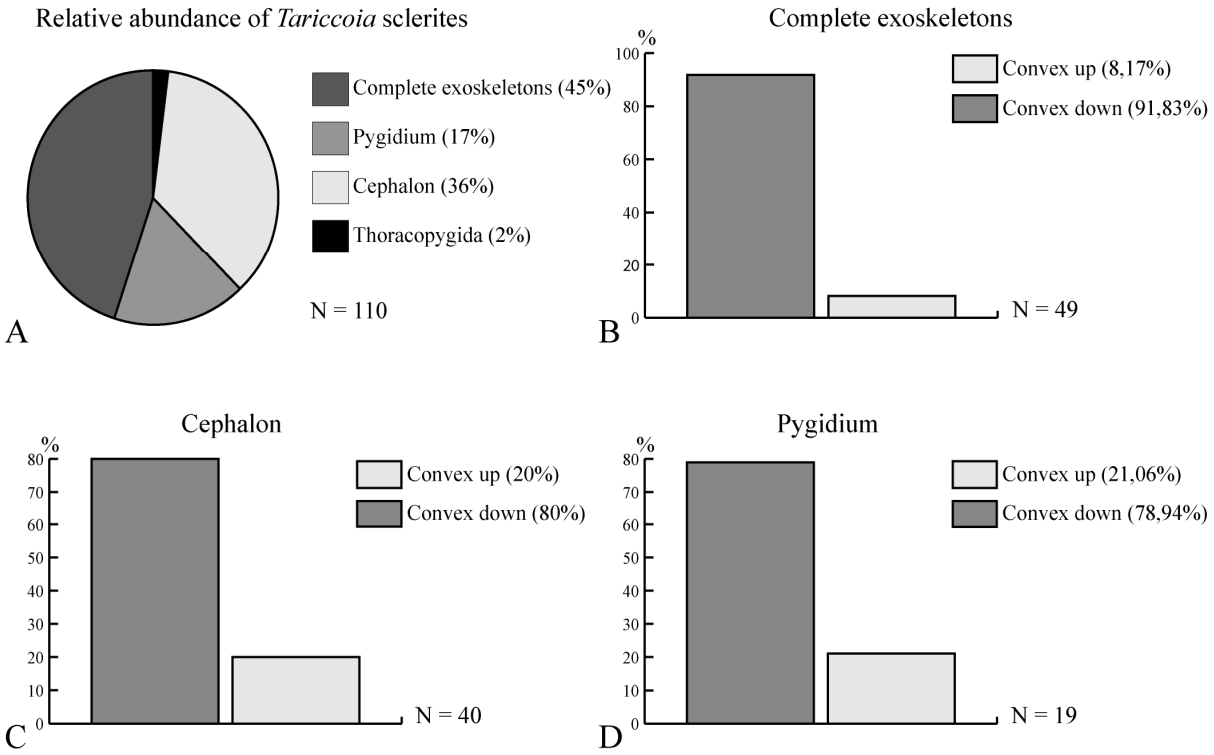

Figure 14. Graphic summarizing the taphonomic data: A) Relative abundance of *Tariccoia* sclerites. B) Dorsoventral orientation of complete exoskeletons. C) Dorsoventral orientation of Cephalons. D) Dorsoventral orientation of pygidia. N indicates the number of sclerites.

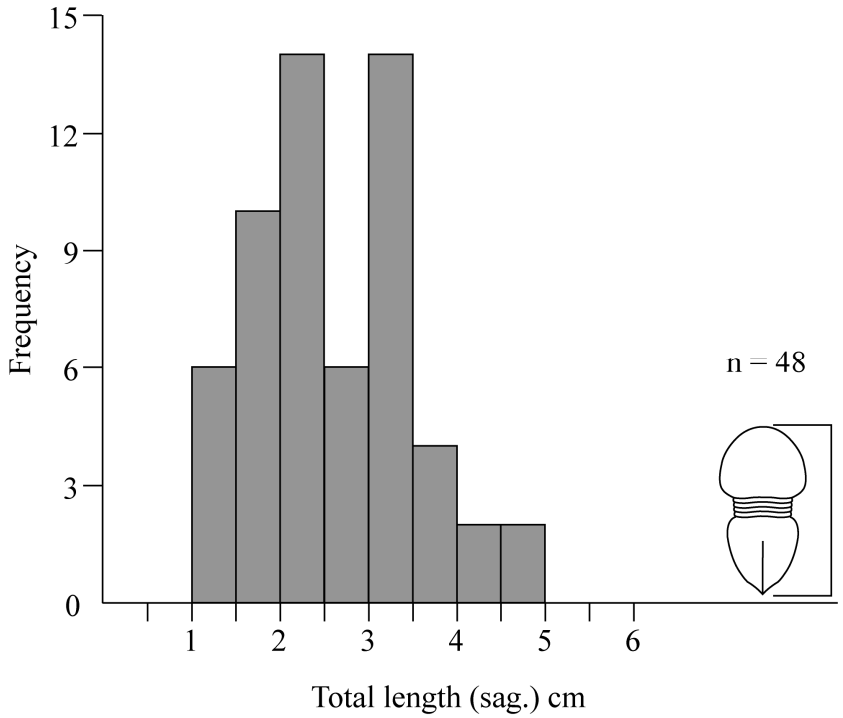

Figure 15. Size-frequency distributions for the high dense assemblage of *Tariccoia arrusensis*. n represents the number of specimens.

2.6. Discussion

2.6.1. Facies interpretation

Facies 1: this conglomerate facies belong to Punta Sa Broccia Member.The clastic sediments of Punta Sa Broccia Member, have been subject to controversial palaeoenvironmental interpretations (Novarese, 1914; Cocozza and Leone, 1977). Martini et al. (1991), on the basis of bed geometry, textures, mineralogical maturity, sedimentary structures, absence of fossils and peculiar facies association proposed for this clastic a continental origin; specifically the conglomerate-muddy intercalations of the upper part of Punta Sa Broccia Member would be interpretable as, supposedly overlapping, shifting fan deltas prograding into relatively shallow water. As general agreement with this interpretation, the facies that characterize the lower portion of the sections measured can be traced back to an environment of distal fan-deltas (McPherson et al., 1987) prograding directly into shallow restricted marine-lagoonal basin.

Facies 2: this facies, characterized by an alternation of massive conglomerates and crudely stratified sandstone, could be related to bed load processes of the overpassing quasisteady turbulent flow (Manville and White, 2003; Zavala et al., 2006, 2011a, b). Vertical variation of grain size (from conglomerates to sandstone), texture and structure (from massive to crudely stratified) could indicate an evolution in flow condition, with changes of drag/shear forces at the base of turbulent flow and variation of fallout

Facies 3: generally the grey siltstones of Riu Is Arrus Member are massive and do not show lamination; this characteristic could have a dual interpretation:

1 - The observations in thin section and cut slab, carried out both parallel and perpendicular to the layers, show a complete homogenization of the sediment which

could be due to intense and pervasive bioturbation. There are several features which provide evidence of bioturbation:

- The scattered recognizable burrows.
- The distinct laminated intervals with the primary bedding often interrupted and disturbed (Ichnofabric index 2, Droser and Bottjer, 1986).
- The uneven distribution of the quartz grains.

These features allow a complete mixing of the sediment and the obliteration of primary sedimentary structures to be considered.

2 - The massive aspect of grey siltstones could be a primary, depositional fabric related to the influx of fine-grained materials transported in suspension and settling from a high concentrated mud cloud which inhibited the segregation of grains and produce poorly sorted and ungraded silt beds (Amy et al., 2006). This interpretation could be inferred from sedimentological and taphonomical data:

- The ungraded aspect of poorly sorted siltstones.
- The low degree of bioturbation as infer by the infrequency of bioturbatory features.
- The absence of evidences of scavenging and bioturbation on the exoskeletons of *T. arrusensis.*
- The high number of articulated arthropod remains.
- The strong preferred dorso-ventral orientation of articulated remains of *T. arrusensis.*

The laminated levels with normal graded beds presumably indicate intervals with low concentrations of silt suspension (Amy et al., 2006).

Facies 4: the parallel lamination with normal graded beds and the absence of traction structures suggest for this facies an origin by normal settling from suspension, with

millimetre/centimetre-thick sand and silt partings reflecting periods of variation in current velocity or sediment supply allowed deposition of coarser sediments.

Facies 5: vertical grain-size change, with alternation of fine sandstone and siltstone which shows both gradation beds and sharp or erosive bed contacts, allows inferring flow fluctuation. The beds with dirty linguiod ripples and climbing ripples reflecting traction by uni-directional current and particle settling concurrently (Jopling and Walker, 1968) while, as the massive gray siltstone interbedded, that usually drapes the bed forms, is conceivable an fallout with a rapid sedimentation rate, that should explain the absence or low bioturbation (Mac Eachern et al., 2005). The coarsening and fining-upward beds indicate an increasing or waxing discharge and decreasing or waning flows, respectively (Mulder and Alexander, 2001; Mulder et al., 2003). Syneresis cracks, which indicate intrastratal shrinkage and can be related to contraction of mud in response to change in the salinity of the surrounding water (Burst, 1965; Pratt, 1988), sporadically occur.

Facies 6: the sandstone/siltstone alternation, with sharp boundaries between the two lithologies, reflects temporal variation in the flow velocity. The medium sandstones appears structureless (massive) at the outcrop scale, and could have originated from gradual aggradation from sustained quasi-steady flow (Kneller and Branney, 1995). The cm-thick coarsening-fining upward sequence, observed in thin section, provides evidence for occurrence of low fluctuation of current velocity in times. The massive siltstone interval presumably settled when the flow stopped.

Stratigraphic position of Riu Is Arrus Member, which is intercalated between the subaerial deposits of Punta Sa Broccia and Medau Murtas Members, allowing to interpret this member as a paralic, protected environment (bay or lagoon).

The lack of subaerial, hypersalin or anoxic evidences indicates connections with marine environment although not back barrier facies was found in the sections measured.

Sedimentologic inferences allow to document a sequence of facies, whose sedimentary features lead to infer fluctuations in the current velocity and fallout rates which could be related to hyperpycnal flows, as subaqueous extension of the fluvial system (Zavala et al., 2006), entering in lagoonal or protected shallow marine setting. Hyperpycnal flows occur when a river in flood discharges a sustained and turbulent mixture of fresh water and sediments more dense than the density of a receiving body of water (Mulder and Alexander, 2001; Zavala et al., 2006; Zavala et al., 2011a, b). Mulder and Syvitiski (1995), document that more than 66% of 230 rivers tested, periodically produce hyperpycnal plume. Hyperpycnal activity is controlled by climate and by drainage basin morphology. It is characteristic for small and medium sized rivers in mountainous environments or in areas with tectonic activity, with low vegetation cover and large temperature ranges. These conditions intensify the erosion and the consequent concentration of the suspended load (Mulder and Syvitiski, 1995; Mulder et al., 2003). Hyperpycnal flows generate a specific sequence of facies with peculiar sedimentary structures mostly related to traction-plus fallout conditions (Zavala et al., 2006, Zavala et al., 2011a, b). Recently Zavala et al. (2010a,b) proposed a genetic facies model for the analysis of hyperpycnal flow deposits. This genetic model identifies three main facies categories related to the three mains processes during the hyperpycnal activity, from bed load (facies B), suspended load (facies S), and lofting (facies L) (Zavala et al., 2011a, b) (Figs. 16 and 17): Facies B (bed load) are the coarsest grained (conglomerates and coarse grained sandstones) and relates to shear and frictional drag

forces provided by the overpassing long-lived turbulent (hyperpycnal) flow; Facies S are finer grained and relates to the gravitational collapse of suspended-load sediments while facies L (very fine sandstones and siltstones) relates to the buoyancy reversal of the hyperpycnal flow.

Following this genetic facies model the facies 2 recognized in the Riu Is Arrus Member could be interpreted as bed load facies (B1 and S1), the facies 5 and 6 could be interpreted as suspended load facies (respectively as S2-S3/L and S1/L) whereas the facies 2 and 3 could be traced to lofting facies (L).

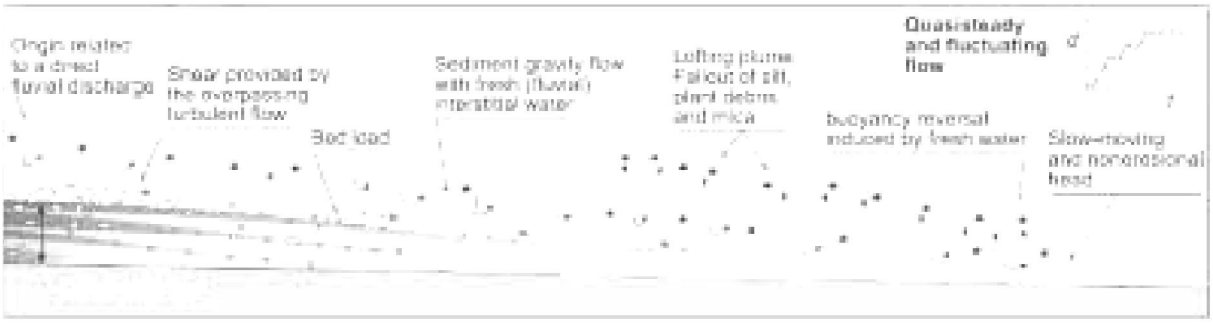

Figure 16. Characteristics of long-lived hyperpicnal flows and their typical processes and deposits (Zavala et al., 2011a, b).

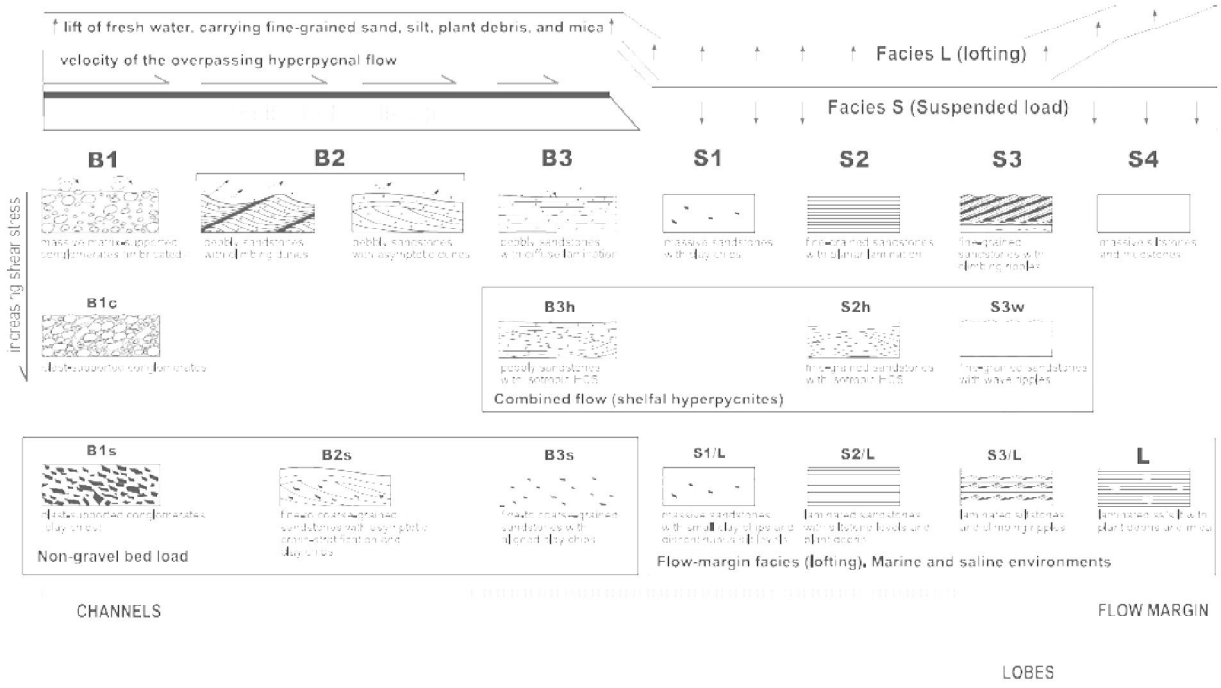

Figure 17. Basic conceptual diagram for the genetic interpretation of clastic facies in hyperpycnal systems. Type B facies relate to bedload processes at the base of an overpassing long-lived turbulent flow. Type S facies originate from the gravitational collapse of sand-sized materials transported in suspension by the turbulent flow. Facies L are composed of very fine grained sandstones interbedded with laminated silts accumulated by fallout from a lofting plume. (Zavala et al., 2011a, b).

2.6.2. Taphonomic interpretation

The analysis of the taphonomic features of *Tariccoia*, which are related to physical (e.g. palaeocurrents) and biological (e.g. predation, bioturbation) processes, allow palaeoecological and palaeoenvironment inferences.

Disarticulation and fragmentation – Actualistic taphonomic experiments conducted on *Limulus polyphemus* (Babcock and Chang, 1997; Babcock et al., 2000), a modern horseshoe crab analog for non-mineralized Palaeozoic arthropods, and other marine arthropods and polychaetes (Allison, 1986; Plotnick, 1986; Briggs and Kear, 1993 and 1994), can help to understand the biostratinomic history and hydrodynamic behaviour of *T. arrusensis*. This actualistic approach reveals that exceptional preservation of non-mineralized and lightly skeletized animals is related both to pre-burial and post-burial condition. The results show that: 1) these animals are remarkably resistant to pre-burial disarticulation and fragmentation, even during turbulent transport, and that 2) disarticulation of poorly mineralized skeletized arthropods seems to proceed at a slower rate than disarticulation of unmineralized (soft-bodied) arthropods. Rapid disarticulation can occur with minimal transport when carcasses are buoyed up from the sediment-water interface by decay gases (postmortem flotation) (Allison, 1986). Experiments conducted on *L. poliphemus* show that internal soft part decay in few days but chitinous sclerites tend to remain articulated for a longer time both in undisturbed and tumbled specimens (Babcock and Chang, 1997). Complete disarticulation occurs after 27 – 40 and 64 days (Babcock et al., 2000. *Tariccoia* remains are characterized by articulated exoskeletons and sclerites which do not show evidence of fragmentation. In agreement with the actualistic experiments, the high degree of articulated remains of *Tariccoia* and the absence of fragmentation could indicate limited transport, minimal reworking on the bottom and short residence time of dead arthropods on the sea bed prior to burial.

Sorting and preferred orientation in plan view – Persistent currents are able to sort arthropod sclerites by size and shape (Hesselbo, 1987) and to impart prominent orientation in plan view to elongate shells (Brett and Baird, 1986). The presence of articulated specimens and sclerites of different size (from 1 cm to 5.6 cm) on the some bedding plane and the random orientation of the *Tariccoia* exoskeletons in plan view allowing to exclude mechanical aggregation and long transport by strong and persistent currents.

Dorso-ventral orientation – Complete specimens of *T. arrusensis* show a preferred convex down orientation. Brett et al. (1999), observed this pattern for the trilobites of the Middle Ordovician beds of the Spillway Member (Rust Formation, New York) and retain that it is the most frequent for the complete specimens.

In order to explain this dorso-ventral orientation and to infer the biostratinomic history of *Tariccoia*, several mechanisms are considered:

1) **The swimming upside-down**: Living arthropods such as *Limulus polyphemus*, swim upside-down, moving their legs and gills to propel themselves. This swimming style can not be rule out for trilobites. Although *Tariccoia* lacks of eyes, some morphological features, such as the streamline shape, the smooth exoskeleton and blunt median tip on the pygidium, could indicate an ability to swim. However the swimming style of the trilobites based on hydrodynamic studies, remains substantially unexplored, with the exception of Fortey (1985).
2) **The falling leaf effect:** The exoskeleton could be lifted up into the water column, e.g. by a mud flow, and, if allowed to settle undisturbed, fall back to the bottom and upside down. It has been experimentally verified (Hesselbo, 1987; Lask, 1993) that the hydrodynamic behaviour of sclerites, related both to the energy environment and to density, size and shape of skeletal elements, controls the transport and orientation.

Usually the sclerites differ in size and shape and thus show different hydrodynamic properties. These hydrodynamic properties, that cause a peculiar convex up/down orientation, may be useful as palaeoenvironmental indicators and especially as current action (Brett and Baird, 1986; Hesselbo, 1987; Speyer, 1987, Lask, 1993). Hesselbo (1987) observed the behaviour of model sclerites of the trilobite *Dikelocephalus* under two hydrodynamic condition: falling (settling) to still water and entrained in flowing water. The cranidium and pygidium, which have different shape, show contrasting attitude. In still water condition, the cranidium denotes a preferred convex-down position (ca. 80 %), in contrast to the pygidium, which assumes a preferred convex-up position. In flowing water a most stable position could not be found for the cranidium while the pygidium shows a most stable inverted position. Field and laboratory experiments with artificial sclerites of the trilobite *Flexicalymene meeki* were made by Lask (1993). The results of these experiments greatly differ from those reported by Hesselbo (1987). In still water condition both the cephalon and pygidium of *Flexicalymene* always settled in a concave-up orientation. Under flowing water the concave-down attitude of sclerites was most stable when either the anterior or side margins faced the current. An experimental study on settling, entrainment and overturning of bivalves and similar geometric models under stagnant and current water, were made by Allen (1984). The settling behaviour is similar in both conditions, with the valves that sink concave-up. The entrainment and overturning thresholds of the convex-up particles are substantially higher than for the same shells convex-down, confirming that the convex-up position is highly stable. These experiments have also shown the effect of suspended sediment to increase the concave-up stability of settling particles. Middleton (1967) denoted a large proportion of concave-up particles for the high concentration flows (40% volume concentration) in experimental turbidity currents

and traced back this pattern to rapid deposition of the bed from suspension and absence of traction along the bottom. Although the conclusions of these experiments could not be directly extrapolated to explain the preferred convex down orientation of *Tariccoia* articulated remains, a settling of exoskeleton from a mud cloud in a quiet environment, might be considered.

3) **The formation of decay gases within the carcasses, which might have flipped the exoskeleton over**: During the decomposition and necrolysis trilobites produced decay gases that cause the buoyancy and the overturning of their exoskeleton (Speyer and Brett, 1985). Paterson et al. (2007) considered this mechanism to explain the inversion of articulated specimens of the Cambrian trilobite *Balcoracania dailyi*. Taphonomic experiments (Allison, 1986; Babcock, 2000), denoted that decay gases cause flotation of freshly killed arthropods for hours to a few days. However, this postmortem flotation induces rapid disarticulation of the carcasses, even with minimal transport (Allison, 1986); therefore the occurrence of high percentage of articulated *Tariccoia* remains allows to exclude this explanation.
4) **The ability of the trilobite to enrol, and consequently to assume most likely the upside down orientation when they died and unrolled as the muscle relax**: Most trilobite had the ability to enrol, presumably as a defence or stress-related mechanism (Brett et al., 1999). As evidenced by Bruton and Nakrem (2005), enrolment is dependent on the mechanism of interpleural articulation which was aided by at least dorsal and ventral longitudinal muscles allowing outstretching and enrolling. Despite of this, *Tariccoia* was not found in enrolled or partially enrolled position. *Tariccoia* has four smooth thoracic segments, which do not show any vincular structure (articular mechanism) between themselves and with the cephalon and pygidium. These observations lead to dismiss this mechanism as a cause of the preferred dorsoventral orientation of *Tariccoia.*

5) **The presence of predators, scavengers and bioturbators**: The upside-down orientation of fully articulated exoskeleton of *Tariccoia* could be due to predation or scavenging activity. However, the fully articulated specimens remains show no evidence of breakage, crushing, boring, tearing, as would be expected if disturbed by scavengers or predators (Babcock, 2003). An intense and pervasive bioturbation is able to completely destroying the primary fabric and forming mottled sediments (Droser and Bottjer, 1986; Miller and Smail, 1997). As pointed by Toots (1965) the reworking of sediments by bioturbation could randomly reoriented the organic remains. Observations on the estuarine and nearshore shelf sediments (Salazar-Jimenez et al., 1982) show that with progressively more intense bioturbation the proportion of horizontal and inclined concave-down bivalves decrease. Within the sediments affected by intense bioturbation (90-100%) the bivalves are predominantly vertical and inclined concave-up oriented. Although the massive aspect of the grey siltstone that containing the *Tariccoia* remains could be due to an intense bioturbation activity that mottled the sediment, the horizontal disposition of the arthropod remains lead to dismiss this hypothesis.

2.6.3. Palaeoecology and depositional history

The origin of the high dense accumulations of *Tariccoia arrusensis* is due by an interplay of palaeoenvironmental, ethological, and sedimentological factors.

The integrated stratigraphic, sedimentologic and taphonomic results leads to interpret the Riu Is Arrus Member as a quiet environment, in a lagoon or bay, periodically affected by hyperpycnal activity. The poor diversity of the fauna which consists of *Tariccoia* and, presumably, algal remains only, point to unfavourable ecological conditions. Trilobites and trilobites-like arthropods were able to occupy marine habitats, from shallow to deep waters (Fortey and Owens, 1999; Fortey, 2004). Therefore the occurrence of *Tariccoia* in a transitional environment, which could be related to local ecological and physical factors (e.g. nutrient supply, current conditions), would confirm the connection with the marine environment.

The occurrence of *Tariccoia* in this unfavourable environment allowing to consider this arthropod as an opportunistic species which, as a general rule, represent species which can adapt to unstable, variable (transient) environments often dominated by physical stress (Levinton, 1970; Dodd and Stanton, 1981).

Several ethological and physical/chemical explanations can be considered to explicate the high concentration of *Tariccoia* remains. Dense clusters of well-preserved trilobites have been reported in literature during the last decades, as denoted by Speyer and Brett (1985), Hughes and Cooper, (1999), Fortey and Owens (1999), Suzuki and Bergström (1999), Karim and Westrop (2002), Chatterton et al. (2003), Paterson et al. (2007), Webster et al. (2008), Gutiérrez-Marco et al. (2009) and Brett et al. (2012).

By analogy with extant marine arthropods, the occurrence of dense groupings could imply gregarious (social) behaviour, including mass molting (synchronous ecdysis),

formation of species-selective spawning aggregations (reproduction) (Speyer and Brett, 1985; Speyer, 1987; Karim and Westrop, 2002) or possibly feeding aggregations (Fortey and Owens, 1999). In other cases principal reasons for clustering in trilobites, could be mechanical aggregations by currents and mass mortality by sporadic anoxic fluctuations (Gutierrez-Marco et al. 2009).

In the case of *Tariccoia*, the high percentage of fully articulated exoskeletons leads one to exclude mass molting and to consider that the high dense fossil accumulation primarily represents the results of a great living abundance.

The observed taphonomic bias of *Tariccoia* remains, may be also due to the gentle transport, rapid burial and low scavengers/bioturbatory activity. It is plausible that the arthropods, whose lifestyle, as discussed by Hammann et al. (1990), was presumably necto-benthic, have been engulfed and transported by rising mud plumes (buoyant plumes). These plume were related to hyperpycnal flows and settled in a quiet environment, entombing the arthropods (Fig. 18). This hypothesis would explain the high concentration of fossils in the siltstone levels immediately above the microconglomerate/sandstone levels and the preferred dorsoventral orientation of the arthropods remains. A rapid, but not instantaneous burial (hours to days), could explain the preservational state of the arthropods, which are mainly articulated but lacking of the appendages, and the dorsoventral orientation of *Tariccoia* in taphofacies tf1. The characteristics of tf 2, such as disarticulation withouth sorting, fragmentation and preferred plan-orientation leading to exclude mechanical aggregation by transport; this taphofacies could be indicative of periods of low sedimentation rates.

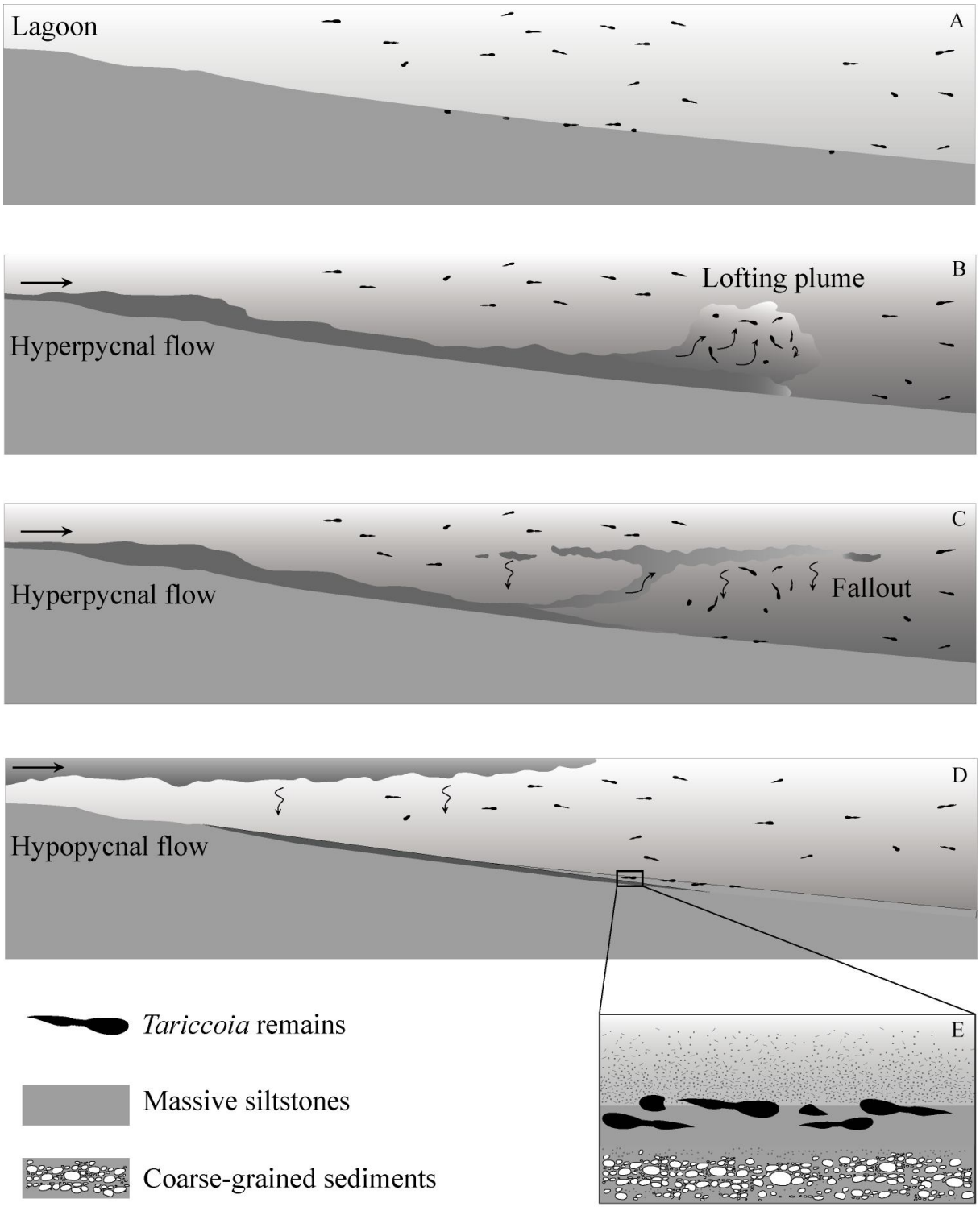

Figure 18. Sketch diagram showing biostratinomic path of *Taricoia*. A) *Taricoia*, which presumably adopted a necto-benthic mode of life, as inferred by the its "well streamlined" shape and lightness, inhabited a quiet lagoonal environment. B) The arthropods have been periodically engulfed and transported by lofting plume, related to hyperpycnal currents. C) The arthropods fallen back to the bottom upside down (falling leaf effect) when the flow stopped and D) rapidly entombed. E) Detailed of the tf1, which consists of high density of articulated arthropod exoskeletons .

2.7. Conclusions

1) Monospecific dense accumulations of the trilobite-like arthropod *Tariccoia arrusensis* was found in locality Roia Srappas, within the Riu is Arrus Member (Monte Argentu Formation).

2) The origin of these arthropod accumulations is related to a combination of a number of ecological (such as gregarious behaviour), palaeoenvironmental and sedimentological factors.

3) Both the stratigraphic position of Riu Is Arrus Member and sedimentological analysis suggest deposition in a very quiet marginal/lagoonal shallow water environment, affected by hyperpycnal flows.

4) The very low biological diversity, allow to infer unfavourable ecological condition and to consider *Tariccoia* as a opportunistic species adapted to inhabit, in a great abundance, a transient, physically stressfull, environment.

5) Detailed taphonomic analysis allow to describe two taphofacies: the first taphofacies (tf1) consists of high density of arthropod exoskeletons and shows that the 92% of the articulated remains of *Tariccoia arrusensis*, which constitute 45% of the total remains, are oriented ventral side-up; the second taphofacies (tf2) is instead characterized exclusively by the accumulation of disarticulated sclerites.

6) The occurrence of the first taphofacies immediately above the microconglomerate/sandstone levels, lead to hypothesized that the arthropods have been periodically engulfed and transported by the mud plumes, related to hyperpycnal flows and fall back to the bottom upside down (falling leaf effect) when the flow stopped.

PART II

ECHINOIDS

Chapter 3.

The Miocene echinoid fauna of Sardinia

3.1. General overview

The Miocene echinoid fauna of Sardinia consists of 30 genera, 18 of which are still present today (60%) (see Table 1). The Miocene fauna mainly consists of irregular forms belonging to the orders Clypeasteroida, Cassiduloida and Spatangoida. The order Clypeasteroida is dominated by the genus *Clypeaster*, with 30 nominal species (Comaschi Caria, 1972), and the extinct sand dollar genera *Amphiope* and *Parascutella*. The regular echinoids are rare and belong to the Cidaroida and Camaradonta, including respectively *Sardocidaris* a subgenus of *Tylocidaris* and the extinct genus *Schizechinus.* None of these genera are present in the Mediterranenan today. The only Miocene echinoids still present in the same area today are the genera *Psammechinus, Echinocyamus, Schizaster*, *Spatangus*, and *Brissopsis*. The difference between the extant and the Miocene echinoid fauna in the Mediterranean area can be related to palaeogeographic and palaeoclimatic events occurred in this area from the late Miocene (Messinian salinity crisis) to the Pleistocene (Pleistocene glaciations).

As discussed by Kroh (2007) the distribution of extant echinoids can be related to sea-surface temperature (SST), particularly for shallow water echinoids. If we assume that the climatic preferences of echinoderms have not change considerably since the Miocene, the distribution of extant genera can be utilized to provide palaeoclimatic inferences. The Miocene echinoid fauna exhibit both extant temperate (e.g. *Spatangus* and *Psammechinus*) and tropical genera. The occurrence in the Miocene fossil record of the Mediterranean area of the genera *Clypeaster*, *Echinolampas*, *Maretia, Lovenia* and *Agassizia,* which are restricted to the tropical region today, and the presence of the extinct sand dollars *Amphiope* and *Parascutella,* whose extant analogous *Echinodiscus*

and *Scaphechinus* live in the tropics today, denote that the palaeoclimate in this region was warm temperate to tropical.

ORDER	FAMILIES	GENERA	EXTANT DISTRIBUTION
Cidaroida	Cidaridae	*Prionocidaris*	Hawaii, Indo-West Pacific
	Psychocidaridae	*Tylocidaris*	Japan
	Rhabdocidaridae	*Rhabdocidaris*	Extinct
Camaradonta	Echinidae	*Stirechinus*	West Atlantic
	Echinometridae	*Parasalenia*	Indo-West Pacific
	Paraechinidae	*Psammechinus*	Atlantic and Mediterranean
	Trigonocidaridae	*Arbacina*	Extinct
	Toxopneustidae	*Tripneustes*	Caribbean, Atlantic, California, Galapagos
		Schizechinus	Extinct
		Lythechinus	Caribbean, Panama, Mexico
Cassiduloida	Echinolampadidae	*Echinolampas*	Japan, Malay and Philippines
	Neolampadidae	*Pliolampas*	Extinct
Clypeasteroida	Astriclypeidae	*Amphiope*	Extinct
	Clypeasteridae	*Clypeaster*	Widespread in tropical region
	Fibularidae	*Echinocyamus*	Indo-Pacific, NE Atlantic, Mediterranean
	Scutellidae	*Parascutella*	Extinct
Spatangoida	Brissidae	*Schizobrissus*	Extinct
		Brissopsis	Indo-Pacific, Atlantic Mediterranean
	Heterobrissidae	*Heterobrissus*	Indo-Pacific and Caribbean
	Loveniidae	*Lovenia*	Indo-West Pacific
	Maretiidae	*Maretia*	Indo-West Pacific
	Macropneustidae	*Macropneustes*	Extinct
		Trachypatagus	Extinct
	Pericosmidae	*Pericosmus*	Widespread in tropical region
	Prenasteridae	*Agassizia*	Caribbean, Saudi Arabia, East Pacific
		Peribrissus	Extinct
	Schizasteridae	*Linthia*	Extinct
		Schizaster	Red sea, Indian Ocean, Mediterranean
		Pseudobrissus	Extinct
	Spatangidae	*Spatangus*	N Atlantic, Mediterranean, South Africa

Table 1. Echinoid fauna of the Miocene of Sardinia based on Comaschi Caria (1972). Systematic based on Kroh and Smith (2010). Distribution data of extant forms baised mainly on Mortensen (1928, 1935, 1940, 1943a, 1943b, 1948a, 1948b, 1950, 1951) and Smith (2007).

3.2. Previous studies

Echinoids are one of the most common and abundant fossil group in the Miocene of Sardinia (Comaschi Caria, 1972). They were studied as early as the second half of the 19th and beginning of the 20th centuries. The first reference to echinoids from the Miocene was by Meneghini (in Lamarmora, 1858). Further studies were conducted by Parona (1887), Cotteau (1985), Lambert (1907-1909), Airaghi (1905, 1915), Checchia Rispoli (1928). A considerable contribution to the study of echinoid fauna of the Miocene of Sardinia was provided by Lovisato who, between the 1909 and 1915, described tens of clypeasteroid species (1909, 1910, 1911a, 1911b, 1911c, 1912a, 1912b, 1913, 1914a, 1914b, 1915a, 1915b). In the second half of the 20th century a revision of the echinoid fauna was provided by Comaschi Caria (1955, 1972). More recent studies on spatangoids were carried out by Stara and Borghi (2012).

All these studies mainly concern the taxonomy of echinoid fauna while the sedimentologic, taphonomic and palaeoecologic aspects of echinoid rich deposits currently are understudied (poorly studied).

3.3. Palaeogeography of western Mediterranean during the Oligo-Miocene

The Tethys was an oceanic realm extended between the Africa/Arabia and India to the south and Eurasia to the north. This ocean connected the Atlantic and the Indo-Pacific oceans until the convergence between the Africa/Arabia and the Eurasian which led to formation of the Alpine chain and the closure of the Tethys with the origin of the Mediterranean and the Paratethys seas (Fig. 19A, B). The timing of this closure and the genesis of the Mediterranean and Paratethys is much debated. As evidenced by Rögl (1999) and Popov et al. (2004) the gateways between the Mediterranean and the Indian Ocean finally closed in the Middle Miocene, after a sequence of openings and closings.

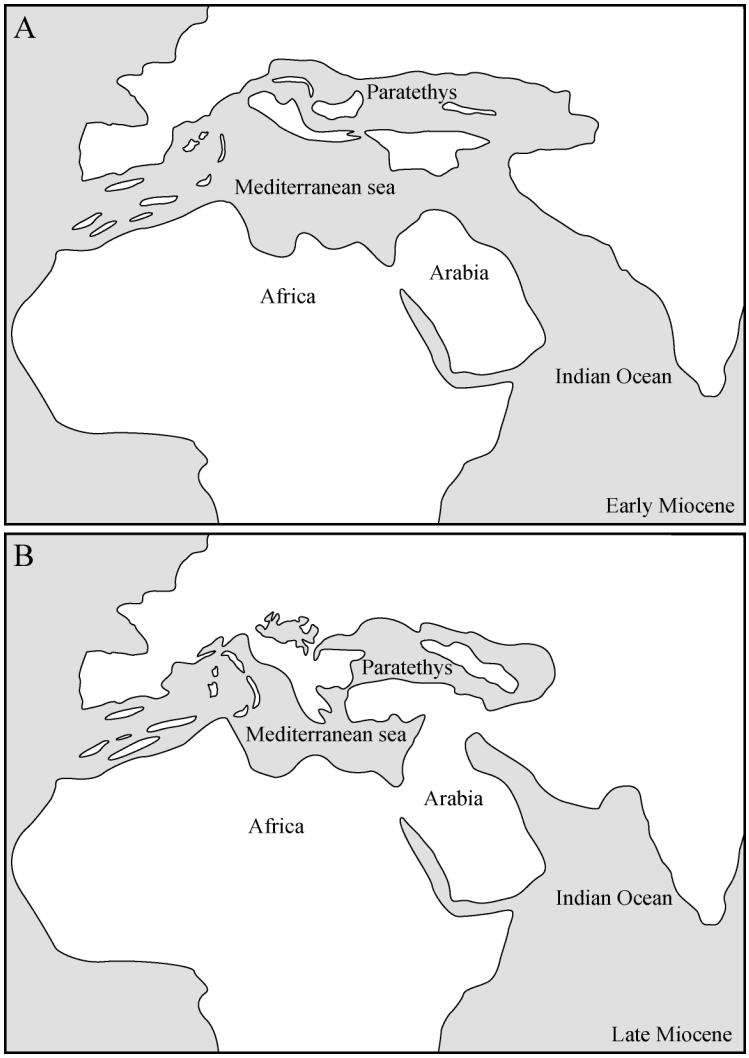

Figure 19. A) Palaeogeography of the Mediterranean and Paratethys during the early Miocene when both the seas possessed open gateways towards the Indian Ocean. B) Palaeogeography of the Mediterranena and Paratethys after finally closure to the Indian Ocean in the late Miocene. After Rögl (1999), modified.

In this palaeogeographic context, between the Oligocene and the Upper Miocene a tectonic activity took placed in the western Mediterranean that caused the opening in different times of two ocean floored basins: the Liguro-Provençal to the West and the Tyrrhenian Sea to the East of the Corsica-Sardinia microblock. Geological and palaeomagnetic data indicate that the Corsica-Sardinia microplate, which up to late Palaeogene was in crustal continuity with the south-east coast of Catalan-Provençal coast (Vigliotti and Langenheim, 1995; Cherchi et al., 2008), undergone a complex geodynamic history with a transition from compressive to extensional tectonics regime and a counterclockwise drifting during the opening of the Liguro-Provençal Basin (Carmignani et al., 1994; Oggiano et al., 1995; Facenna et al., 2002; Lustrino et al., 2009) (Fig. 20). The origin, the beginning and the end of both tectonic regimes and the rotation of the Corsica-Sardinia microblock are still objects of debated (Fig. 20). Carmignani et al. (1994) suggest that a compressive phase, affected the Sardinia during the Late Oligocene-Aquitanian.

This compressive phase, related to the Northern Appennines collisional tectonics, revealed itself with NE-SW strike-slip tectonics which consisted of transpressional and transtensional structures which are evident in the North-Eastern part of Sardinia (Oggiano et al., 1995). A later extensional phase, connected with the collapse of the Appennines orogen, caused the spread of the Liguro-Provençal basin and the origin of the Sardic rift ("Fossa Sarda" Auct.) during the Late Aquitanian-Early Burdigalian.

Cherchi and Montadert (1982) and Cherchi et al. (2008) proposed a different geodynamic scenario, suggesting that an extensional regime affected the Iberia-Europe region since the Late Oligocene as a consequence of the Appennine west-dipping subduction zone; these authors believe that a rifting phase, which started in the Rupelian and ended during the Aquitanian (23-24 Ma), involved Sardinia prior the anticlockwise rotation.

It has been proposed that the rotation of the Sardinia-Corsica microplate started between 21.5 Ma (Gattaceca et al., 2007) and 19 Ma (Speranza et al., 2002), although other authors such as Gueguen et al. (1998) suggest that this rotation started in the Chattian, ca. 25 Ma. The end of the drifting was between 15 Ma (Vigliotti and Langenheim, 1995) and 10 Ma (Gueguen et al., 1998). The engine of this tectonic activity is controverse (see Lustrino et al., 2009 and references cited); Facenna et al. (2002) e.g. believe that the Liguro-Provençal Basin is a classical back arc basins which could be related to a north-west directed, east retreating subduction system while Mantovani et al. (2002) traced to the origin of this basin to lateral expulsion of crustal wedge.

More recently Viti et al. (2009) proposed that the Liguro-Provençal basin originated between the Late Miocene and the Langhian, by the east-south eastward extrusion of the wedge of the Alkapeca Belt.

The Oligo-Miocene sedimentary succession of Sardinia appears to be related to this complex tectonic evolution. This sedimentary sequence consists of three main cycles (Fig. 21) and is characterized by continental, transitional and marine facies, accompanied by volcanic activity.

As discussed by Assorgia et al. (1997) and Spano and Barca (2002), the first sedimentary cycle can be related to the Oligocene-Early Miocene trascurrent tectonic while the sediments of the second and third sedimentary cycles were accumulated in an extensional tectonics regime within the NNW-SSE Sardinian rift.

A different interpretation is provided by Cherchi et al. (2008) which evidenced a tectonic control on depositional sequences and indicate a syn-rift sedimentation, which is represented by the first sedimentary cycle and a post-rift sequence which corresponds to the second sedimentary cycle.

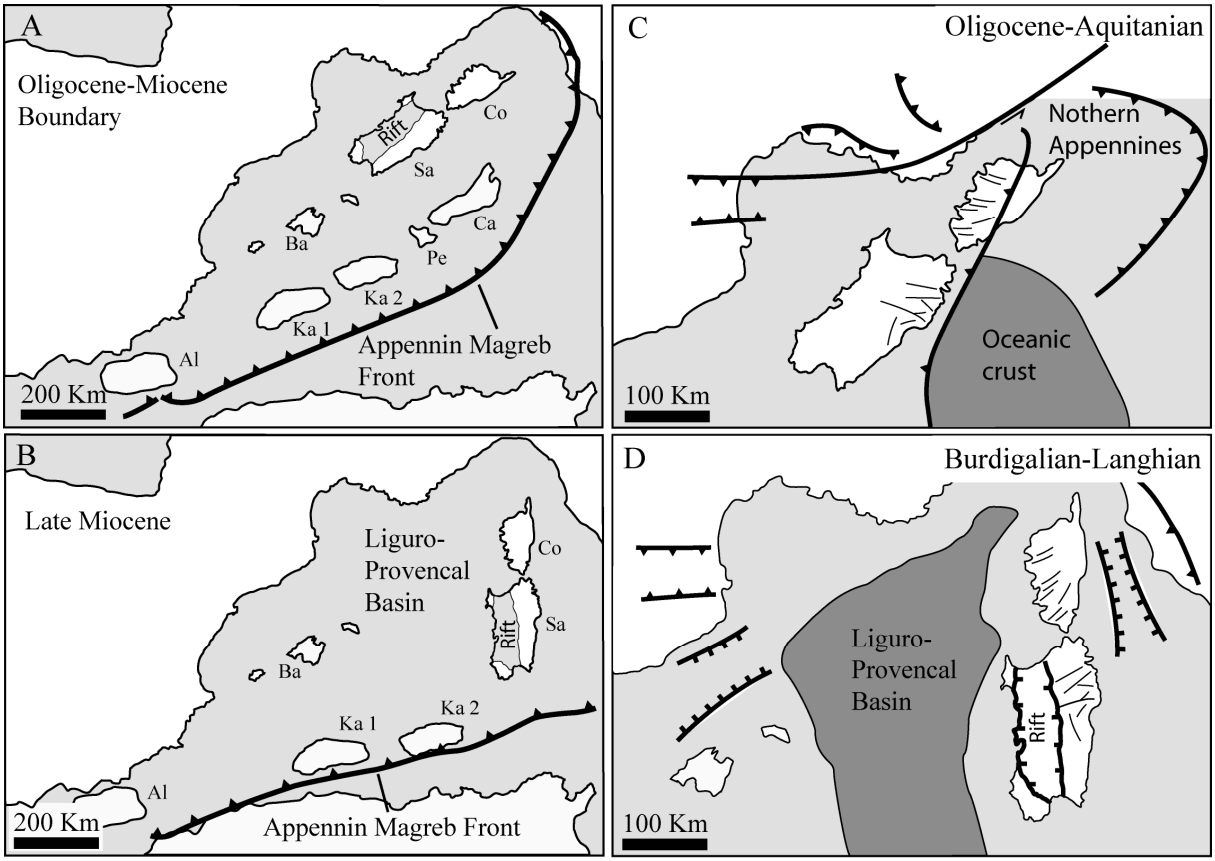

Figure 20. A) Geodynamic and palaeogeography of the western Mediterranean region during the Oligo-Miocene boundary. B) Palaeogeography of the western Mediterranean region during the late Miocene. Sa: Sardinia; Co: Corsica; Al: Alboran; Ka1 and Ka2: Great and Litlle Kabylies; Pe Peloritani Mountains; Ca: Calabria. After Lustrino et al. (2009), simplified. In this geodynamic scenario the rifting stage prior to the counterclockwise rotation of Sardinia. C) Geodynamic reconstruction of Sardinia and Corsica position during the Oligo-Miocene boundary with the development of a strike-slip tectonic, related to the Nothern Appennines collision; D) An extensional phase caused the spread of the Liguro-Provençal basin and the origin of the Sardic rift (Fossa Sarda Auct.) during the late Aquitanian-lower Burdigalian; from Carmignani et al.

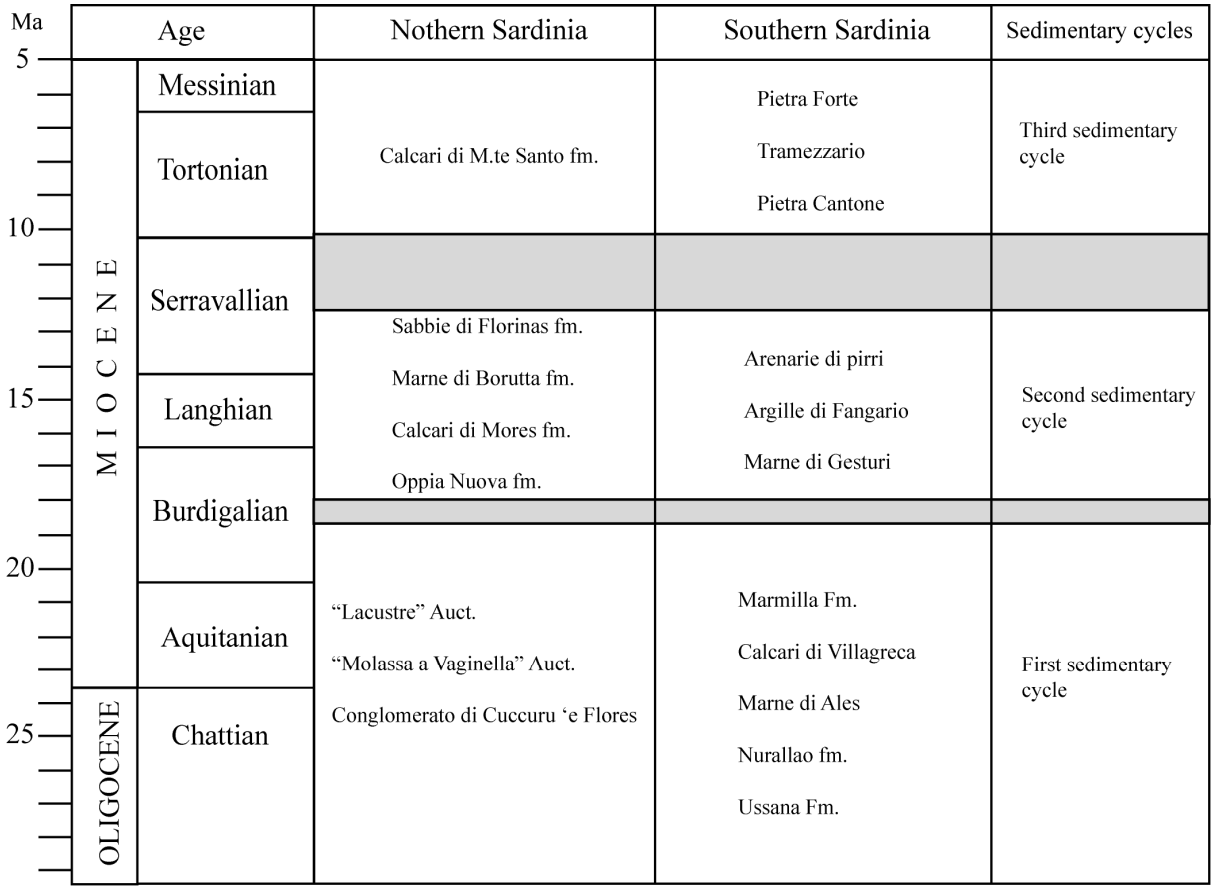

Figure 21. Lithostratigraphy of the Oligo-Miocene sedimentary cycles of Nothern and Southern Sardinia; blue boxes indicates uncertainty in age determination. After Carmignani et al. (2001), modified.

3.4. Taphonomy and sedimentology of echinoid mass accumulations

This second part of the work mainly concerns the study on the taphonomy and sedimentology of irregular (clypeasteroids and spatangoids) and regular echinoid mass accumulations in order to clarify their origin and to utilize them within the scope of further palaeocological and palaeoevironmental investigations.

Three main aspects promote the taphonomic and sedimentologic study of fossil echinoids:

1) Echinoids have an extensive fossil record. As evidenced by Smith (1984) echinoid are one of the latest classes of echinoderms to evolve. The first undisputed echinoid appears in the Upper Ordovician but the diversity of echinoids during the Palaeozoic appears low because both of the low preservation potential and the adaptation of these epifaunal deposit feeders to limited variety of habitats. The echinoids rapidly diversified and underwent a spectacular adaptative radiation during the Mesozoic with the rapid evolution and diversification of the irregular echinoids (Kier, 1982) whose diversity increase during the Cenozoic.
2) Echinoids are common members of the marine benthic community in a wide variety of extant environments. Currently there are about 1000 living species of echinoids (Kroh and Smith, 2010; Kroh and Mooi, 2012), which inhabit a wide array of marine habitat, from the high to low latitude and from the litoral to abyssal zone, although they reached the greatest diversity and abundance in shallow shelf areas. This aspect promoted a suite of ecological and actuopalaeontological studies which have taphonomical, palaeoecological and palaeoenvironmental implications.
3) Echinoids, which possessing a multi-plated skeletons composed of a large number of high-magnesium calcite elements, are potentially good indicators of biostratinomic processes. Actuopalaeontological studies based on laboratory and

field observations have contributed to clarify the taphonomic processes affecting their skeletons after death (Allison, 1990; Kidwell and Baumiller, 1990; Greenstein, 1991; Nebelsick and Kampfer 1994; Nebelsick, 1999). These studies have shown that the preservation of echinoids is related to both intrinsic factors such as constructional morphology including the architecture of test, nature of connective tissues and extrinsic factors such as temperature, oxygen content, bacterial activity, transport mechanisms and scavengers.

Chapter 4.

Sedimentology and palaeoecology of mass accumulations of clypeasteroid echinoids from the Miocene of Sardinia

Although clypeasteroid echinoid mass accumulation are common in the shallow water sediments of the Miocene of Sardinia, they have received little attention as far as their origin is concerned. In this chapter, four clypeasteroid mass accumulations from the Lower Miocene of Sardinia are studied and compared in order to understand their genesis and palaeoecology.

4.1. General overview on the morphology of Clypeasteroids

The Order Clypeasteroida consists of hundreds living and fossil species of irregular echinoids commonly known as sand dollars, key hole and cake urchins (Mooi, 1989, Smith, 2007). These irregular echinoids appear in the Late Palaeocene/Early Eocene; Kroh and Smith (2010) believe that the clypeasteroids are a monophyletic clade which evolved neotenously from the paraphyletic cassiduloids. The clypeasteroids realized a spectacular evolution both in time and in palaeogeographic space (Seilacher, 1979) and rapidly diversified and specialized, reaching a cosmopolitan distribution during the Miocene. In this period all extant families evolved and came to replace cassiduloids as the main echinoid group in inshore clastic facies.

The Parathethys and Mediterranean area were characterized by a rapid radiation of the clypeasteroids during the Oligo-Miocene as documented by their extremely good fossil record; they are mainly represented by the genus *Clypeaster*, which lives in the tropical regions today, and the extinct genera *Amphiope*, *Parascutella* and *Scutella*. As discussed by Seilacher (1979) and Smith (1984) clypeasteroids even realized an

ecologic evolution which consisted of several innovation in their morphology and feeding techniques. Currently the genus *Togocyamus*, from the Late Palaeocene of West Africa and Nigeria (Kier, 1982), is the most primitive clypeastroid known. *Togocyamus* is a small-size genus (less than 1 cm length) with high test profile and subglobular shape; these clypeasteroid shows incipient petals, periproct on the aboral surface, the absence of food grooves and only an adradial line of pores with relatively few tube feet per plate (Kier, 1982) (Fig. 22).

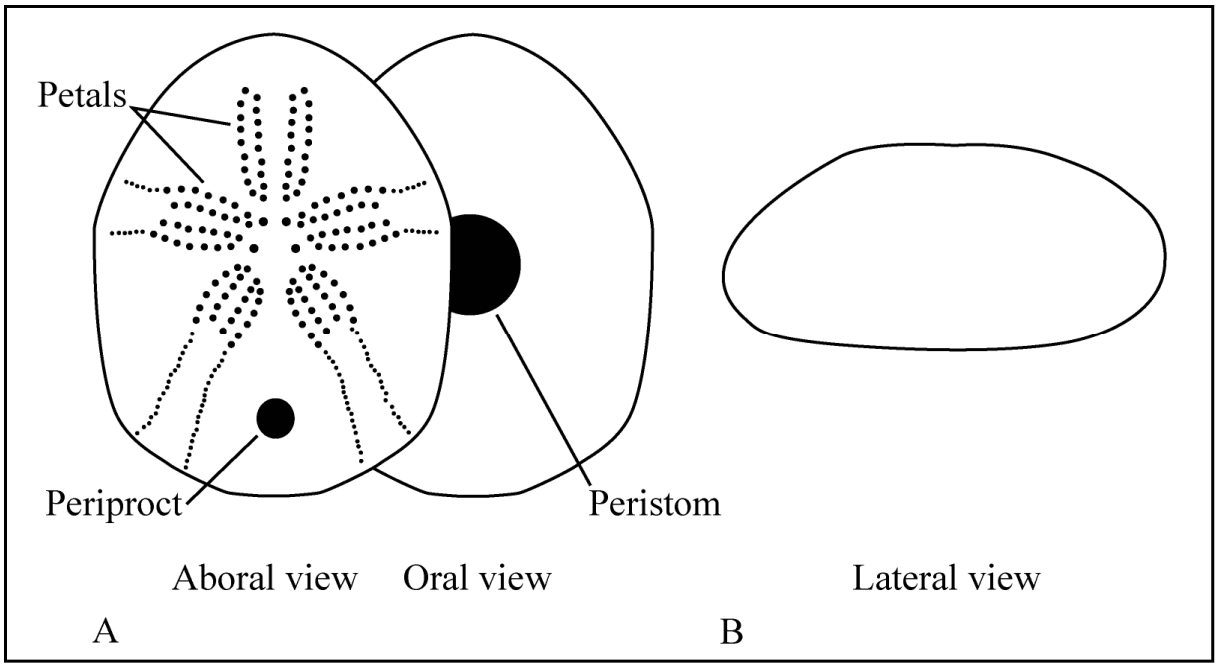

Figure 22. External morphology of *Togocyamus* from the Late Palaeocene; currently this genus is considered the most primitive clypeasteroid known.

Morphological changes, such as flattening of the test and development of food grooves, petals, internal supports and large number of minute tube feet occurs (see Fig. 23). As discussed by Seilacher (1979) these innovations allowed clypeasteroids, particularly sand dollars, to adopt a shallow burrowing, sieve feeding mode of life in high energy, sandy, shoreface environments. A few forms of clypeasteroids, such as the extant *Clypeaster rosaceus* and, by analogy, some fossil well-shaped, highly vaulted *Clypeaster,* such as *Clypeaster altus* secondarily returned to an epibenthic mode of life.

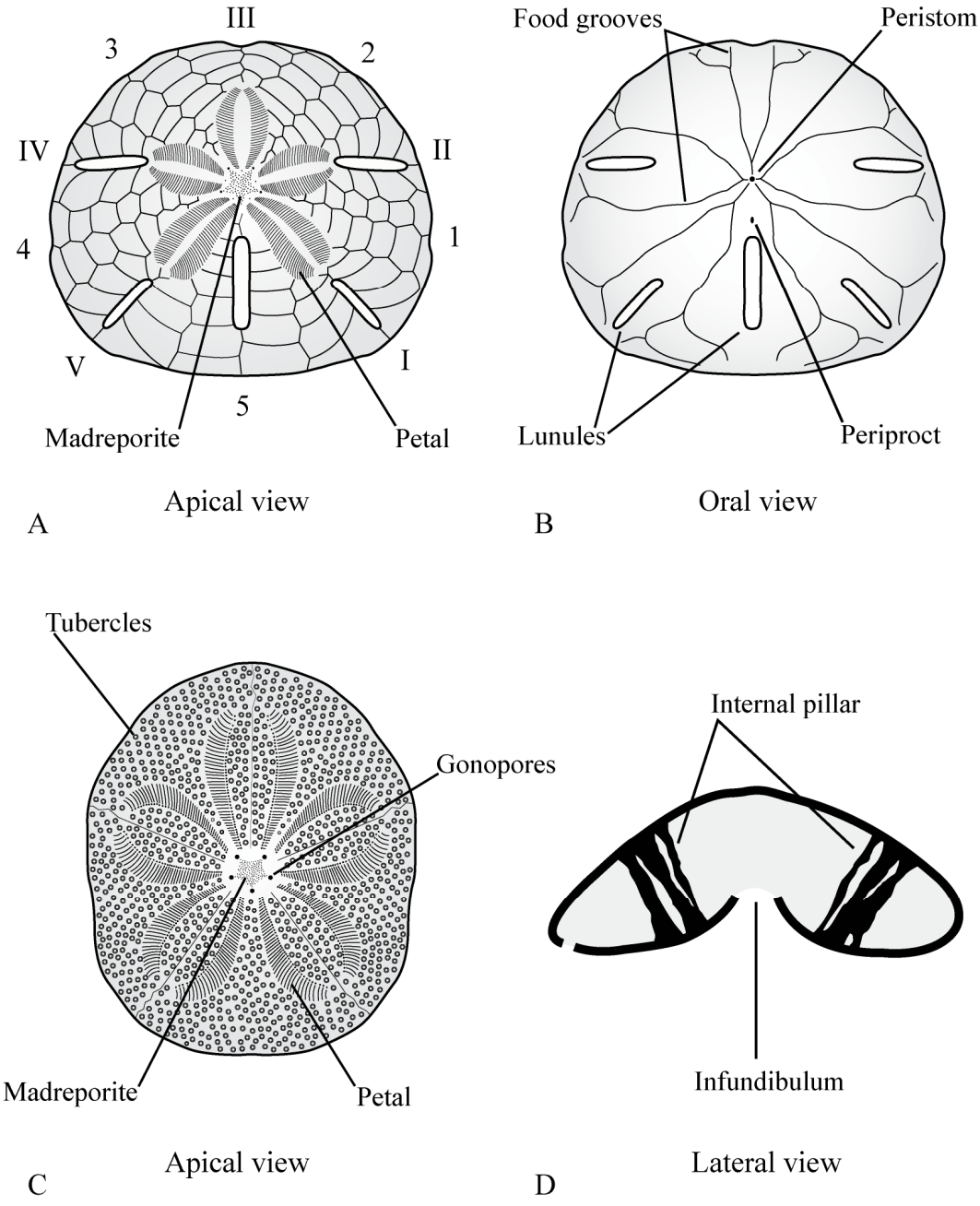

Figure 23. A, B) General external morphology of the extant sand dollar *Mellita quinquiesperforata*. Roman numbers indicate the ambulacral columns while Arab numbers indicate interambulacra columns; C) General external morphology of *Clypeaster rosaceus*; D) Schematic lateral section of *Clypeaster rosaceus* showing

4.2. Mass accumulation of Clypeasteroids

Extinct sand dollars such as *Amphiope*, *Parascutella* and *Scutella* are frequently found in mass deposits, the so-called "*Scutella* sands" especially in the Oligo-Miocene of the Mediterranean and Paratethys area (Nebelsick and Kroh, 2002). Despite their widespread distribution and their importance within both siliciclastic and carbonate sedimentary sequences, fossil sand dollar mass accumulations, which vary highly with respect to taxonomic composition, taphonomic signals and sedimentological features, have received little attention. This also holds true for the commonly occurring deposits of sand dollar from the Miocene of Sardinia with the exception of Stara et al. (2012), who have recently provided a general overview on the geological and palaeoecological features of the *Amphiope* deposits of Sardinia.

This study focused on four clypeasteroid accumulation beds from the Lower Miocene of Sardinia. Two accumulation beds are dominated by the genus *Amphiope* with subordinate *Parascutella*. A third accumulation is dominated by the genus *Parascutella* with subordinate *Clypeaster* while the fourth clypeasteroid mass accumulation show similar percentages of *Amphiope* and *Clypeaster*. Fossil clypeasteroid genera exhibit a high morphological variability which often needs a detailed taxonomic revision due to high phenotypic variations of species as well as differing taxonomic concepts among authors (e.g. Rose and Poddubuik, 1987; Kroh, 2005). Comaschi Caria (1955, 1972) listed 9 species of *Amphiope* and 30 species of *Clypeaster* in a revision of the Miocene echinoid fauna of Sardinia. The taxonomic analysis of the clypeasteroid species of Sardinia is beyond the scope of this study which concerns the taphonomy, sedimentology and palaeoecology of sand dollars accumulation beds.

Fossil clypeasteroid echinoids can frequently occur in mass accumulations as emphasized by Nebelsick and Kroh (2002), who list more than twenty published records of sand dollar concentration of various genera such as *Amphiope*, *Encope*, *Laganum*,

and *Parascutella* from the Early Eocene to the Pliocene. Further occurrence of clypeasteroid concentrations mainly characterized by the genus *Parascutella*, *Clypeaster* and *Amphiope* have recently been described in the Late Oligocene of Croatia (Mikša, 2009), in the Middle Miocene of Tarragona (Belaústegui et al., 2012) and in the Late Miocene of Sicily (Garilli et al., 2010). The genesis of these deposits is related to a number of factors including the population ecology of living animals, their robust test morphologies leading to high preservation potentials and environmental conditions (e.g. Seilacher, 1979; Moffat and Bottjer, 1999; Nebelsick, 1999; Nebelsick and Kroh, 2002; Belaústegui et al., 2012).

Sand dollars inhabit tropical to temperate, often agitated, shallow water environments (Ghiold and Hoffman, 1986). They live in sandy and muddy-sandy bottoms and include both deposit feeding endobenthic forms, such as *Echinodiscus*, *Encope*, *Mellita*, *Scaphechinus* and suspension feeding forms such as *Dendraster*. Two ecological aspects which potentially play an important role in generating shell concentrations are 1) gregarious behaviour, and 2) mass mortalities. Gregarious behaviour can lead to very high densities: mass occurrences of hundreds or even thousands of individuals per square meter are reported for *Mellita quinquiesperforata*, *Encope grandis*, *Dendraster excentricus* (Salsman and Tolbert, 1965; Chia, 1969; Merril and Hobson, 1970; Ebert and Dexter, 1975 - see compilation in Nebelsick and Kroh, 2002). Recent studies have also documented high density populations in other genera such as *Scaphechinus* from Japan, which reach quantities of more than 300 individuals per square meter (Takeda, 2008). The high-density sand dollar communities can generate decimetre-thick mounds and undergo periods of mass mortality as documented by Salsman and Tolbert (1965) for *Mellita quinquiesperforata* and Takeda (2008) for *Scaphechinus mirabilis*.

Shell accumulations can result from autochthonous in situ biological accumulations, be the result of concentrating transport mechanism or be diagenetic in origin (Kidwell, 1991). Shell concentrations can furthermore represent discrete events, be condensed and hiatal in origin or be of a composite nature. As discussed by Kidwell and Jablonski (1983) the origin of shell accumulation is, in general, a function of the rates of skeletal hardpart input and sedimentation rates. The genesis of mass accumulations can be complex involving factors relating to original populations densities, hydrodynamics of transport and post-depositional alterations (e.g. Fürsich and Pandey, 1999). Skeletons as sedimentary clasts behave differently from their siliciclastic counterparts with varying effect of biogenic grain shapes and densities on transport and settling velocities (Maiklem, 1968; Behrensmeyer, 1975). Specific factors affecting the hydrodynamic behaviour of sand dollars include their flat test and the presence of lunules or ambital indentation in some genera (Seilacher, 1979; Telford, 1981).

4.3. Geological setting

The Oligo-Miocene sedimentary succession of Sardinia is located within the NNW-SSE orientated Sardinian Basin, a tectonic trough that extends from the Gulf of Sassari in the northwest to Cagliari in the south (Figs. 24A and 25A). Three main sedimentary cycles are recognized within the Sardinian Basin, the origin of which is a subject of much debate (Assorgia et al., 1997; Cherchi and Montadert, 1982; Carmignani et al., 2001; Funedda et al., 2000; Lecca et al., 1997). The sediments of the basin show a wide range of both terrestrial and marine facies and can be highly fossiliferous as shown by the three sections containing the mass occurrences of clypeasteroids studied here. Two clypeasteroid assemblages are found in the Sarcidano region in central Sardinia within the Late Oligocene-Burdigalian Nurallao Formation which belongs to the first sedimentary cycle of the Sardinian Basin. A third assemblage is located in the Logudoro region of northern Sardinia (Fig 1A) in the Late Burdigalian Calcari di Mores Formation and belongs to the second sedimentary cycle.

4.3.1. Cuccuru Tuvullau and Duidduru sections (Sarcidano - Central Sardinia)

The two sand dollar assemblages from the the Sarcidano region of central Sardinia are found in the localities Cuccuru Tuvullao, about 1.5 km NE of Nuragus (N39°47’19’’ – E9°34’77’’) (Fig. 24A, C), and Duidduru, about 1.5 km W of Genoni (N39°47’32’’ – E8°59’14’’) (Fig. 24A, B). Both assemblages are found within the Lower Miocene sediments of the Nurallao Formation along the eastern edge of the Sardinian Basin. In the Sarcidano area, the predominately clastic Oligo - Miocene sequence rests above a Palaeozoic and Mesozoic basement. The Cenozoic sequence starts with the Late Oligocene to Early Aquitanian Ussana Formation (Pecorini and Pomesano Cherchi, 1971) consisting of polygenic conglomerates, breccias, sandstones and volcanoclastic sediments of continental origin (Cherchi et al., 2008). The Ussana Formation is partly heteropic with and is followed by the Late Oligocene to Burdigalian Nurallao Formation

(Funedda et al., in press), originally named the “Gesturi Sandstone” (Cherchi, 1974). This formation is subdivided into two members: 1) the basal Conglomerato di Duidduru member formed by polygenic heterometric conglomerates with interbedded sandstones which have been assigned to a deltaic environment (Sowerbutts and Underhill, 1998); and 2) the Sabbie di Serra Longa member in which the studied sand dollar accumulations are found. These sediments include sandy-conglomerate alternations followed by fossiliferous sandstones and sandy limestones which can be traced to shoreface environments. The Nurallao Formation is partially heteropic with and followed by the Calcari di Villagreca and the Marmilla Formation. The Calcari di Villagreca sediments can be traced to a shallow, high energy, carbonate ramp and are dated to the Late Oligocene to Early Burdigalian. The Marmilla Formation, which consists of a thick volcano-sedimentary sequence, represents the deeper shelf setting, and is micropalaeontologically dated to the Late Aquitanian to Early Burdigalian. The Calcari di Villagreca and the Marmilla Formation are unconformably followed by the Gesturi Marls (Cherchi, 1974; Cherchi, 1985) the upper part of which has been dated to the Middle Langhian using microfossils (Cherchi, 1974; Iaccarino et al., 1985).

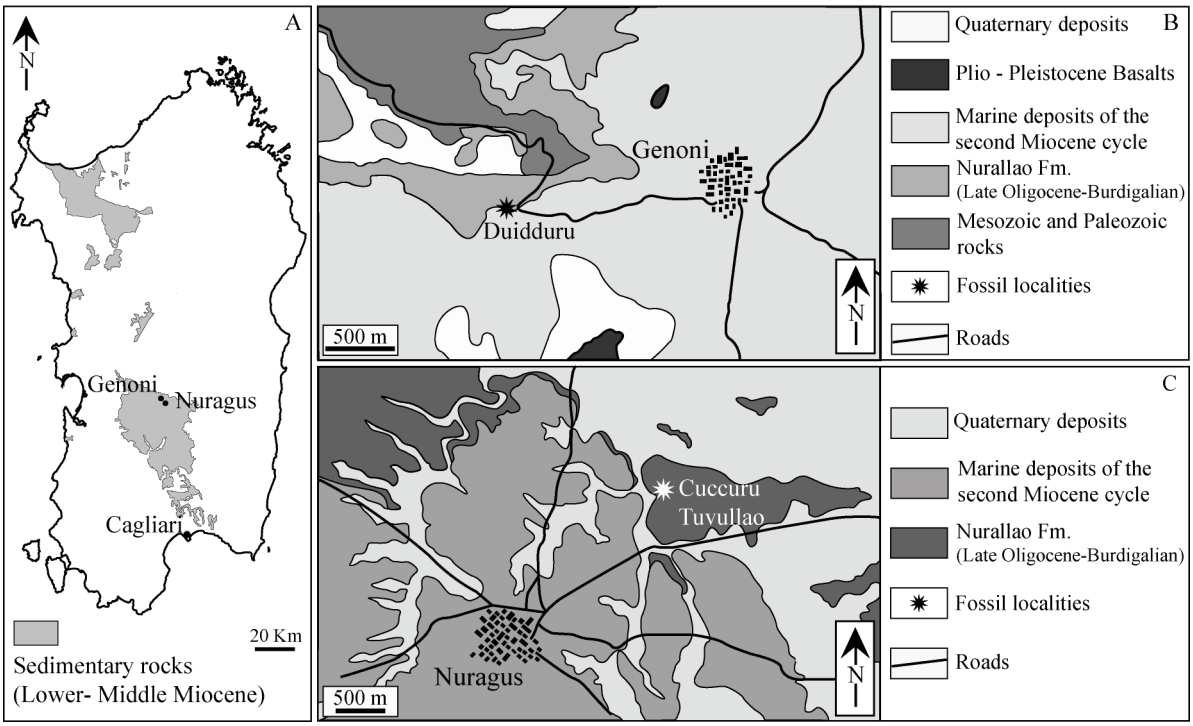

Figure 24. A) Outcrop distribution of Lower-Middle Miocene sedimentary rock in Sardinia. B) Simplified geological map of the Genoni area with the location of Duidduru fossil locality. C) Simplified geological map of the Nuragus area with the location of Cuccuru Tuvullao fossil locality. The asterisks indicates the location of studied clypeasteroid assemblages.

4.3.2. Monte Sa Loca and Ardara sections (Logudoro-northern Sardinia)

The other two investigated clypeasteroid assemblage from the Logudoro region (northern Sardinia) are found at the base of the Monte Sa Loca hill, east of the village of Chiaramonti (N40°44'55'' – E8°50'1'') and 200 m south of the village of Ardara (N40°36'55'' – E8°48'29'') within the Calcari di Mores Formation (Fig. 25A, B, C). The Lower to Middle Miocene trangressive succession of Logudoro is found within the Sardinian Basin complex which in northern Sardinia consists of generally NNW to N-S striking half grabens (Funedda et al., 2000). In this area, the sedimentary deposits of the second Miocene cycle unconformably overlie a volcanic succession consisting of Early Burdigalian rhyolitic to dacitic pyroclastic flows (Lecca et al., 1997). The succession starts with lacustrine sediments followed by fluvio-deltaic conglomerates and litharenitic sands of the Oppia Nuova Formation (Funedda et al., 2000). The following Calcari di Mores Formation consists mostly of stratified bioclastic limestone and subordinate quartz rich, fossiliferous, poorly cemented sands. This sandy facies, which contains the echinoids studied here, is of shallow water origin (Mazzei and Oggiano, 1990; Funedda et al., 2000). The Calcari di Mores Formation is followed by the Marne di Borutta Formation containing calcareous clayey siltstones, sands and marls representing a deeper shelf facies. The Marne di Borutta Formation is unconformably followed by the Sabbie di Florinas Formation which has been interpreted as formed in fluvial, lacustrine and brackish coastal environments (Funedda et al., 2000).

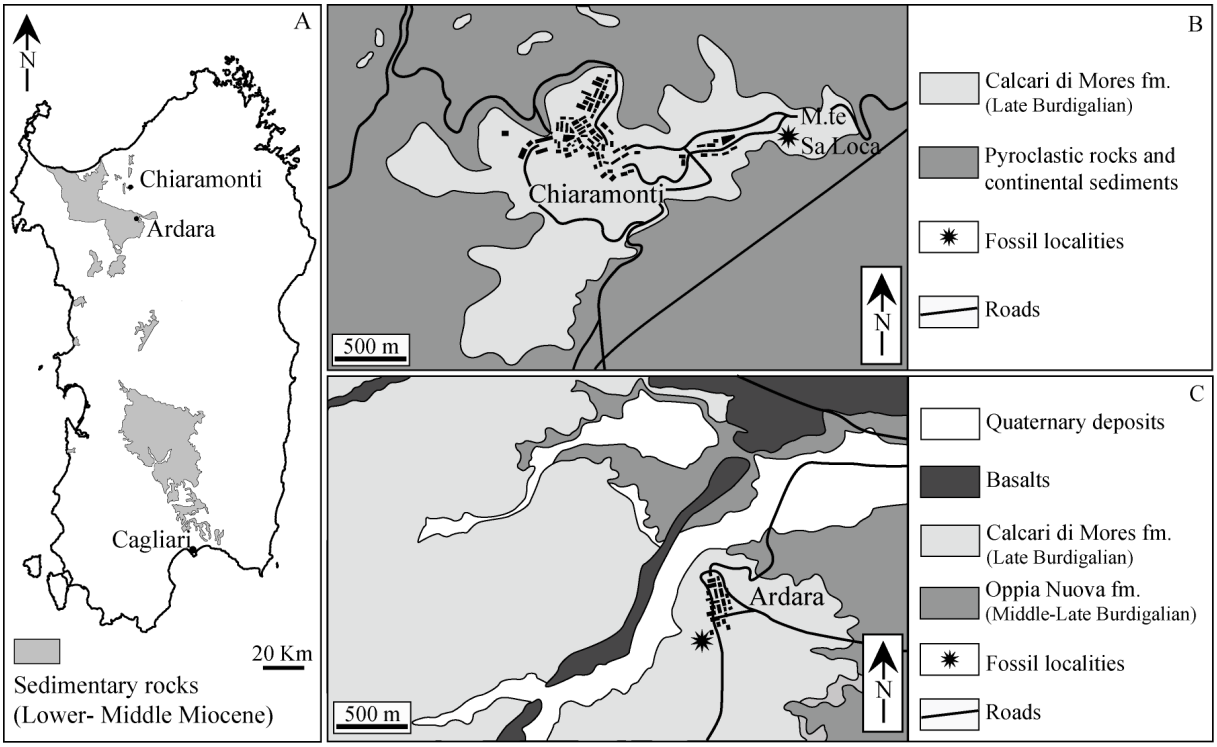

Figure 25. A) Outcrop distribution of Lower-Middle Miocene sedimentary rock in Sardinia. B) Simplified geological map of the Chiaramonti area with the location of Monte Sa Loca fossil locality. C) Simplified geological map of the Aradara area with the location of the fossil locality. The asterisk indicates the location of studied clypeasteroid assemblages.

4.4. Material and methods

An intense stratigraphic, sedimentological, palaeontological and taphonomic field and laboratory study was made. On each site, vertical sections were measured and a detailed facies analysis conducted recording sedimentological and palaeontological features supported by thin section analysis. The composition, diversity and abundance of fossils were observed for each section. Recorded taphonomic signatures of echinoids include disarticulation, fragmentation, abrasion and encrustation. The fabric of the mass accumulations was analysed by recording the orientation of fossil material relative to the bedding in both plan and cross section. Collected specimens are housed in the Department of Earth Sciences of Cagliari University.

4.5. Stratigraphy and sedimentology

4.5.1. Cuccuru Tuvullao section (Nuragus)

Five facies are recognized in the stratigraphic section measured at Cuccuru Tuvullao (Fig. 26) within the Serra Longa member, from the base to top:

Facies A consists of 50 to 80 cm-thick heterometric, polymictic conglomerates, containing sub-rounded to rounded clasts with a maximum size of 20 cm. The clasts consist predominantly of metamorphic, granitic and subordinate carbonate pebbles from the Palaeozoic and Mesozoic basement. These conglomerates are massive and are predominantly supported by a sandy matrix. The pebbles are frequently encrusted by barnacles. The upper bed contact is sharp.

Facies B consists of a 2.5 m-thick bed of poorly sorted, medium to coarse sandstones containing abundant granules, pebble and cobbles (Figs. 27A, B, C).The pebbles and cobbles ranging in size from 4 to 10 cm are sub-rounded to rounded and have the same mineralogical composition as the underlying facies. These massive sandstones contain floating granules and pebbles.

Fossils consist mainly of irregular echinoids belonging to the genera *Amphiope* (Figs. 27B, C) and *Parascutella*. Barnacles found in this facies both encrust pebbles and are reworked. The upper bed contact is gradual.

Facies C shows a maximum thickness of 5 m and consists of richly fossiliferous deposits supported by a very fine sandy matrix. The fossil content is dominated by gastropods belonging to the genus *Turritella* and the bivalve *Panopea*. Sand dollars fragments are found in the lower part of this facies. The upper contact is sharp and erosive.

Facies D is formed by 80 cm-thick heterometric, polymictic, massive conglomerates with sub-rounded to rounded clasts with a maximum size of 10 cm. These clasts consist predominantly of metamorphic, granitic and carbonate pebbles in a predominantly

sandy matrix. Fossil components include echinoderms such as *Echinolampas* and pectinid bivalves. The bed contact with facies E is sharp.

Facies E is the characterized by massive, medium grained sandstone with a maximum thickness of 2 m. The fossil content includes bivalves belonging to genera *Flabellipecten* and *Ostrea* and echinoids such as *Clypeaster*, *Echinolampas* and spatangoids.The most frequent echinoid genus of this facies is the cassiduloid *Echinolampas* which frequently show evidence of encrustation by serpulids.

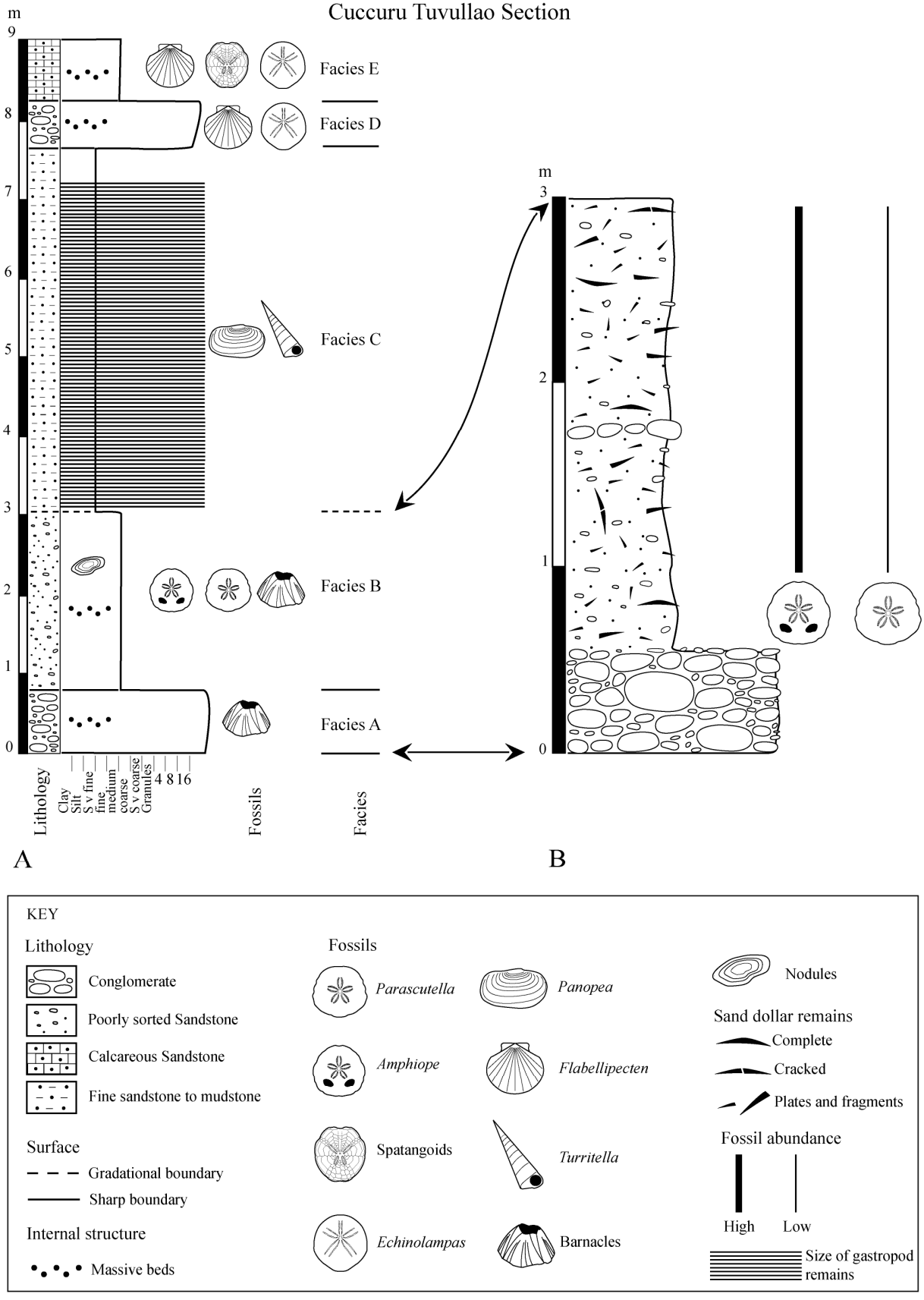

Figure 26. A) Stratigraphic section of Cuccuru Tuvullao (Nuragus). B) Detailed section of sand dollar deposit.

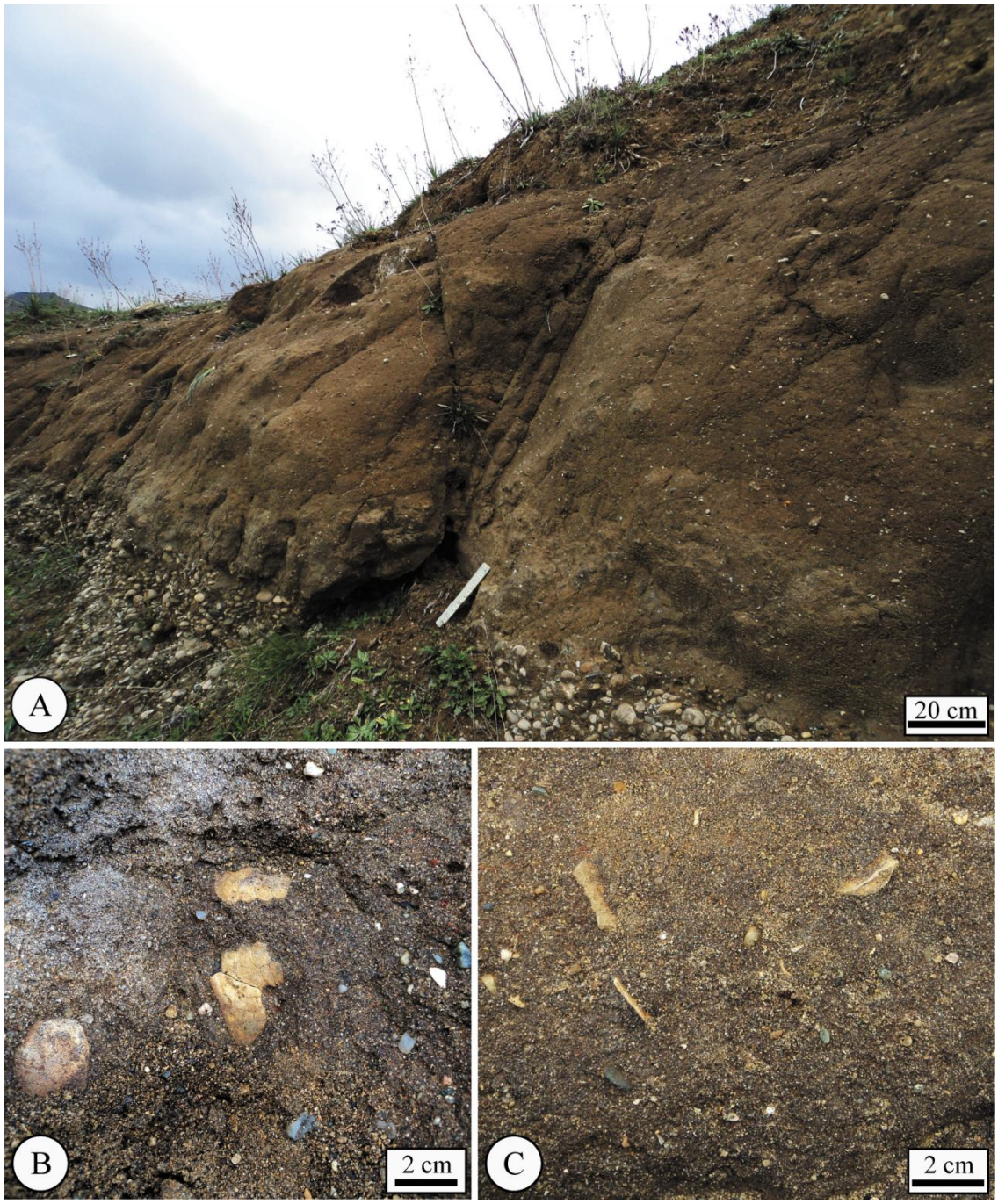

Figure 27. Cuccuru Tuvullao (Nuragus): A) Detail of the Cuccuru Tuvullao section showing the sand dollar deposit (Facies B), which lies on the conglomeratic facies (Facies A); B) and C) Coarse sandstone with *Amphiope* remains (Facies B).

4.5.2. Duidduru Section (Genoni)

Five facies are found in the Duidduru locality consisting of a clastic succession within the Serra Longa Member of the Nurallao Formation (Fig. 28). From the base to top:

Facies A consists of a m-thick, poorly cemented, well sorted, medium to coarse, massive sandstone. Fossils consist mainly of clypeasteroid echinoids belonging to the genera *Parascutella, Amphiope* and *Clypeaster*. Reworked barnacles and vertical burrows are also found. The upper bed contact is sharp and erosive.

Facies B consists of 110 cm-thick, moderately sorted, massive sandstones containing abundant quartz granules and bioclasts. The sub-rounded to rounded 2 mm to 5 mm large quartz granules float within the sandstones. Fossil components include the irregular echinoids *Parascutella*, *Clypeaster* and *Echinolampas*, bivalves, such as *Flabellipecten* and gastropods (Fig. 29A, B). The bed contact with facies C is gradual.

Facies C is 80 cm-thick and consists of poorly cemented, well sorted, medium-coarse massive sandstones. The upper bed contact is gradual.

Facies D consists of ca. 80 cm to 1 m-thick, weakly cemented, massive fine sandstones to siltstones. Fossils consist of the gastropod *Turritella*, bivalves and spatangoid remains. The bed contact with facies E is sharp.

Facies E is characterized by well sorted, well cemented, massive medium sandstones reaching a thickness of about 3 m. Sporadic burrows and argillaceous nodules occur.

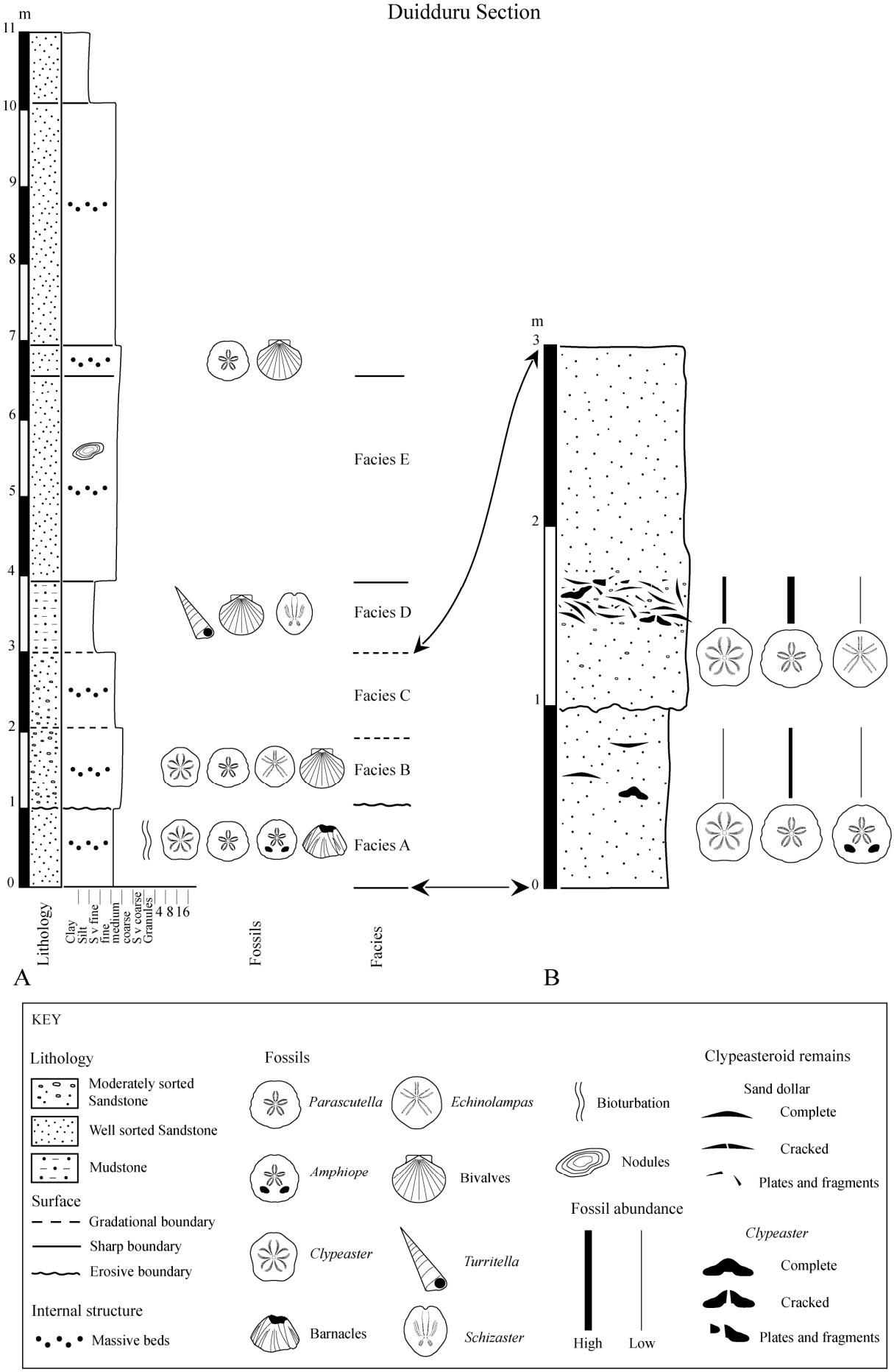

Figure 28. A) Stratigraphic section of the Serra Longa Member of the Nurallao Formation, Duidduru (Genoni). B) Detailed section of the clypeasteroid deposit.

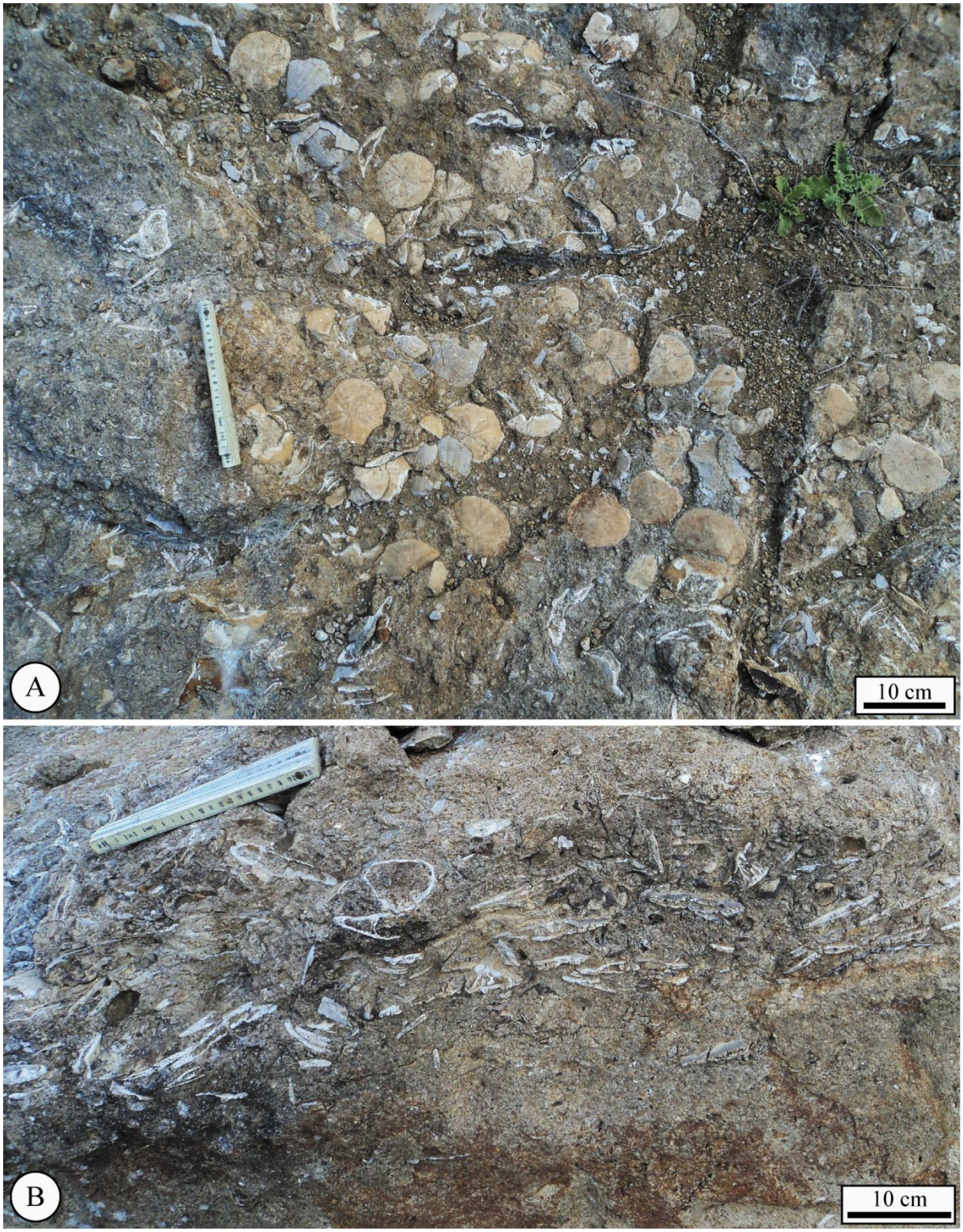

Figure 29. Duidduru (Genoni): A) Detail of the Duidduru section showing the sand dollar mass accumulation bed (Facies B); B) Detail of sand dollar assemblage.

4.5.3. Monte Sa Loca section (Chiaramonti)

The Monte Sa Loca Section (Fig. 30) consist of 9 m of Miocene sediments within the Calcari di Mores Formation. Five sedimentary faciesare present from the base to top:

Facies A consists of a m-thick very fine, weakly cemented, massive calcareous sandstone. Sporadic internal moulds of microgastropods occur. The contact with facies B is gradual.

Facies B is a 80 cm-thick quartzo-feldspatic, poorly sorted, massive sandstone with a carbonate cement. Pebbles within the sandstone range in size from 1 to 4 mm, are sub-rounded to sub-angular, and consist of 85 % quartz, 15 % feldspar and very rare plagioclase grains. The contact with facies C is gradual.

Facies C is a m-thick and consists of very coarse, poorly sorted, massive sandstone with carbonate cement. The pebbles range in size from 1 to 4 mm, are sub-rounded to sub-angular, and consists of 80 % quartz and 20 % feldspar. Fossils are represented by irregular echinoids belonging to genera *Amphiope*, *Parascutella* and *Agassizia*. The upper bed contact is gradual (Fig. 31A, B).

Facies D consist of a 20 cm-thick, massive, matrix supported conglomerate. The pebbles range in size from 2 to 8 mm, are sub-rounded to sub-angular and consist of 55% quartz and 45% feldspar. Sporadic sand dollar fragments occur. The upper bed contact is gradual.

Facies E is very similar to facies B but differs in the fossil content which consists of very rare sand dollar remains. The upper bed contact is sharp.

Facies F is composed of 50 cm-thick fine calcareous sandstone. Fossils consist mainly of the sand dollars *Amphiope* and *Parascutella* and bivalves belonging to the family Arcidae and Cardiidae.

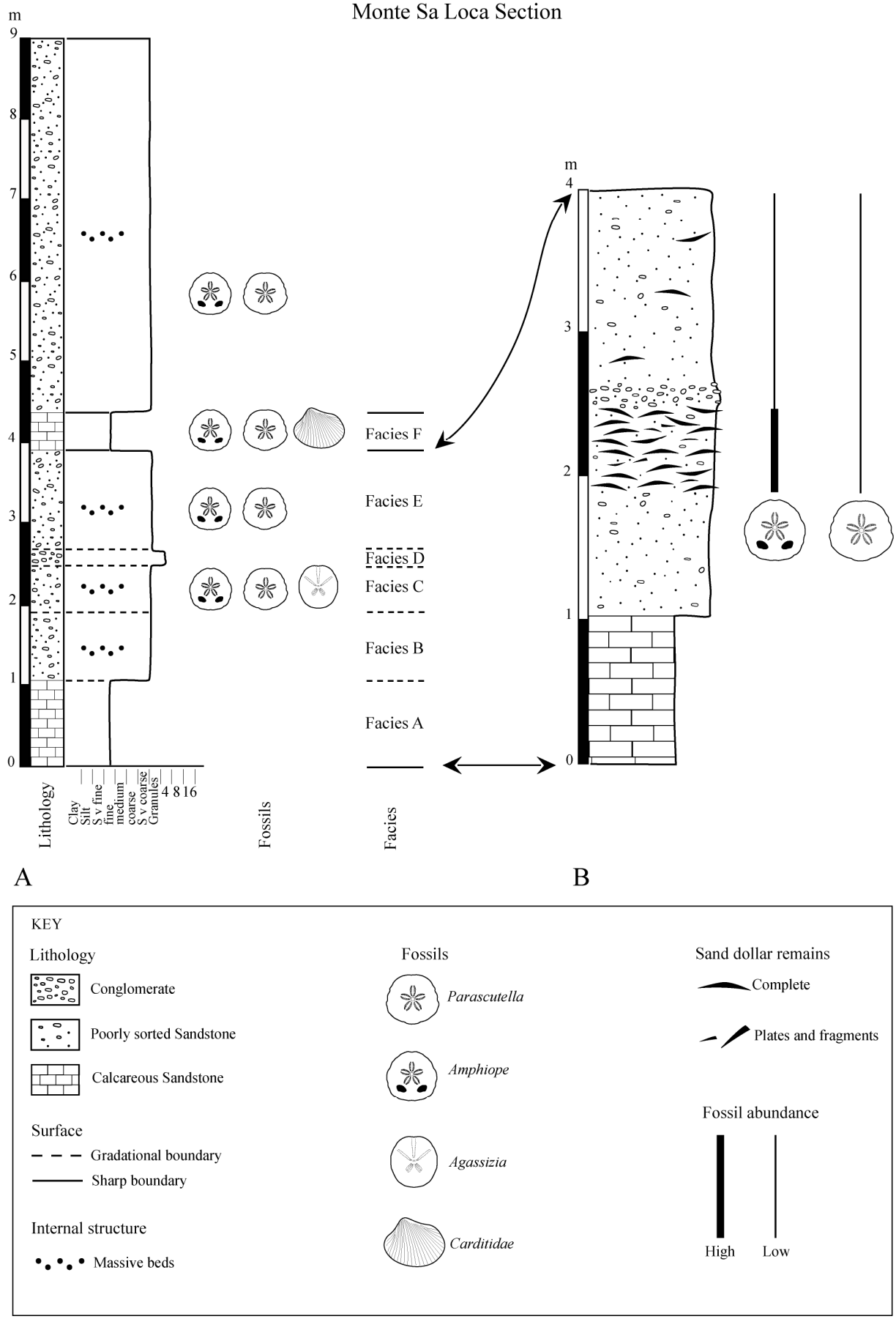

Figure 30. A) Stratigraphic section of Monte Sa Loca (Chiaramonti). B) Detailed section of sand dollar deposit.

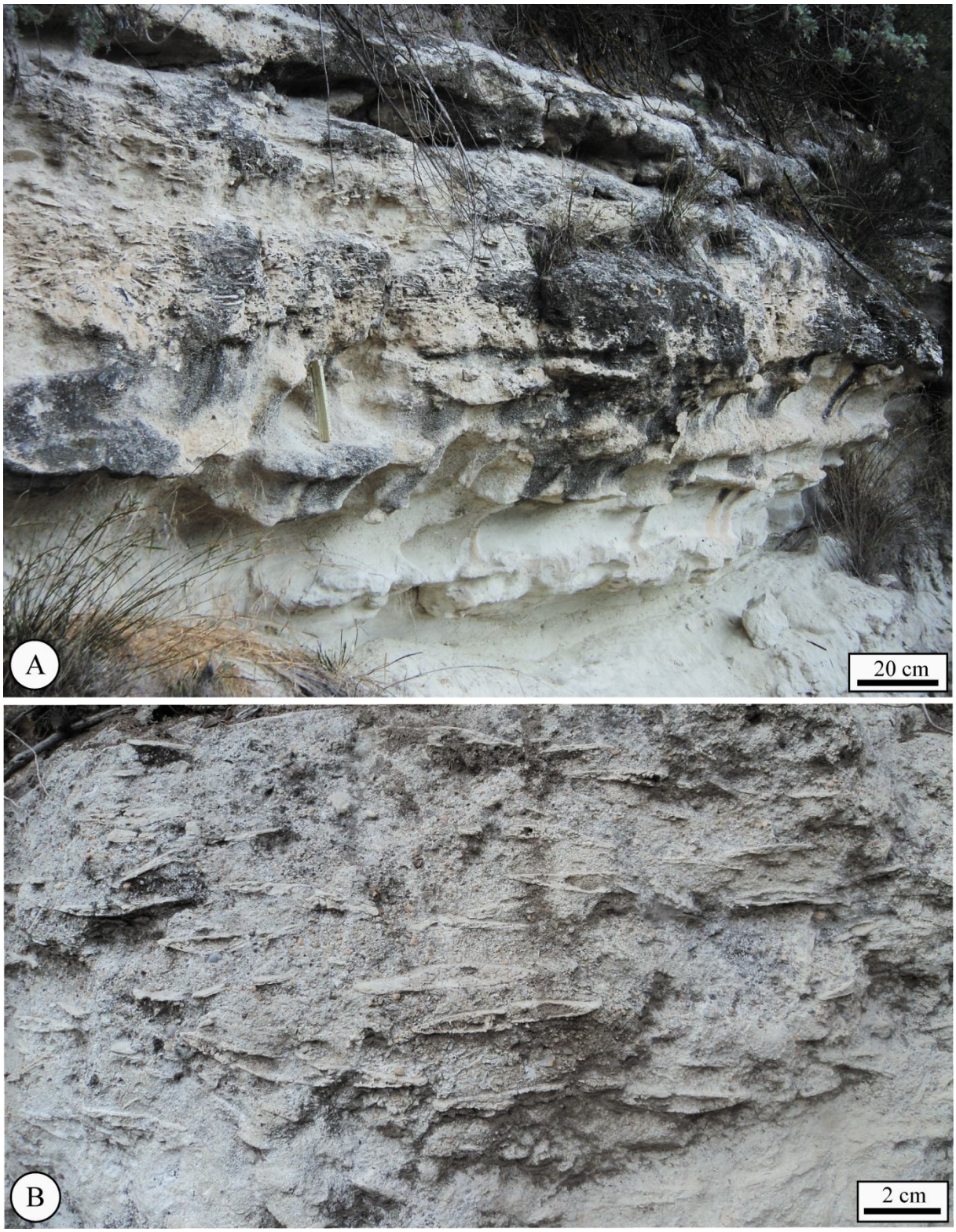

Figure 31. Monte Sa Loca (Chiaramonti): A) Detail of the Monte Sa Loca section showing the sand dollar mass accumulation bed (Facies C); B) Detail of sand dollar assemblage.

4.5.4. Ardara section

The Ardara section (Fig. 32) consists of 10 m of Miocene sediments within the Sabbie di Florinas Formation. Seven sedimentary facies are present from the base to top:

Facies A consists of a 2 m-thick, poorly sorted, massive conglomerate with carbonate cement. The pebbles which range in size from 2 mm to 1 cm, are sub-rounded to sub-angular, and consists of 70 % quartz and 30 % feldspar. Within these conglomerates discontinuous interbedded conglomerate levels with large pebbles (from 2 to 5 m) occur. The upper bed contact is gradual.

Facies B is a 2 m-thick very fine sandstone with lenses of very coarse sandstones. These fine sandstones are intensely bioturbated. The upper contact is gradual.

Facies C is a 30 cm-thick, oligomictic conglomerates (Fig. 33A, B, C), containing sub-rounded to rounded clasts with a maximum size of 5 cm. The clasts consist predominantly of granitic and quartz pebbles. These conglomerates are massive and are predominantly clast supported. The fossil content consists of *Amphiope* and *Clypeaster* remains and reworked barnacles. The upper bed contact is sharp.

Facies D is a 30 cm-thick and consists of very coarse, poorly sorted, massive sandstone with carbonate cement. The pebbles range in size from 1 to 4 mm, are sub-rounded to sub-angular, and consists of 90 % quartz and 10 % feldspar. These sandstones contain floating granitic and quartz pebbles with maximum size of 5 cm. Fossils are represented by irregular echinoids belonging to genera *Amphiope* and *Clypeaster*, pectinids and reworked barnacles. The upper bed contact is gradual.

Facies E is composed of a m-thick very coarse, massive, sandstones with very abundant calcareous algae. The granules, which range in size from 1 to 2 mm, are sub-rounded to sub-angular, and mainly consist of quartz. The upper bed contact is gradual.

Facies F is a 2 m thick limestone with floating quartz granules. The fossil content consists of large oysters.

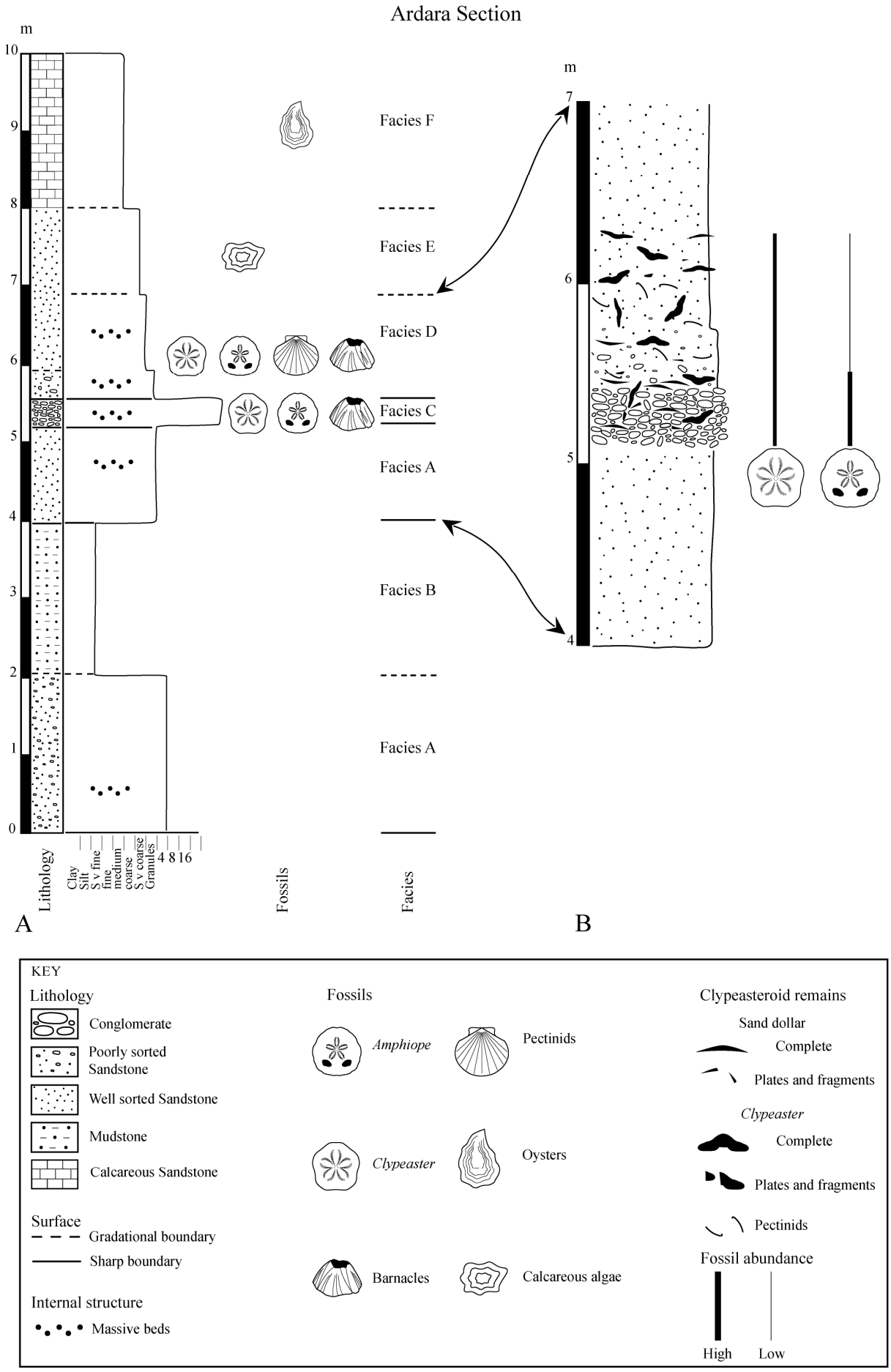

Figure 32. A) Stratigraphic section of the Calcari di Mores Formation, Monte Sa Loca (Chiaramonti). B) Detailed section of the sand dollar deposit.

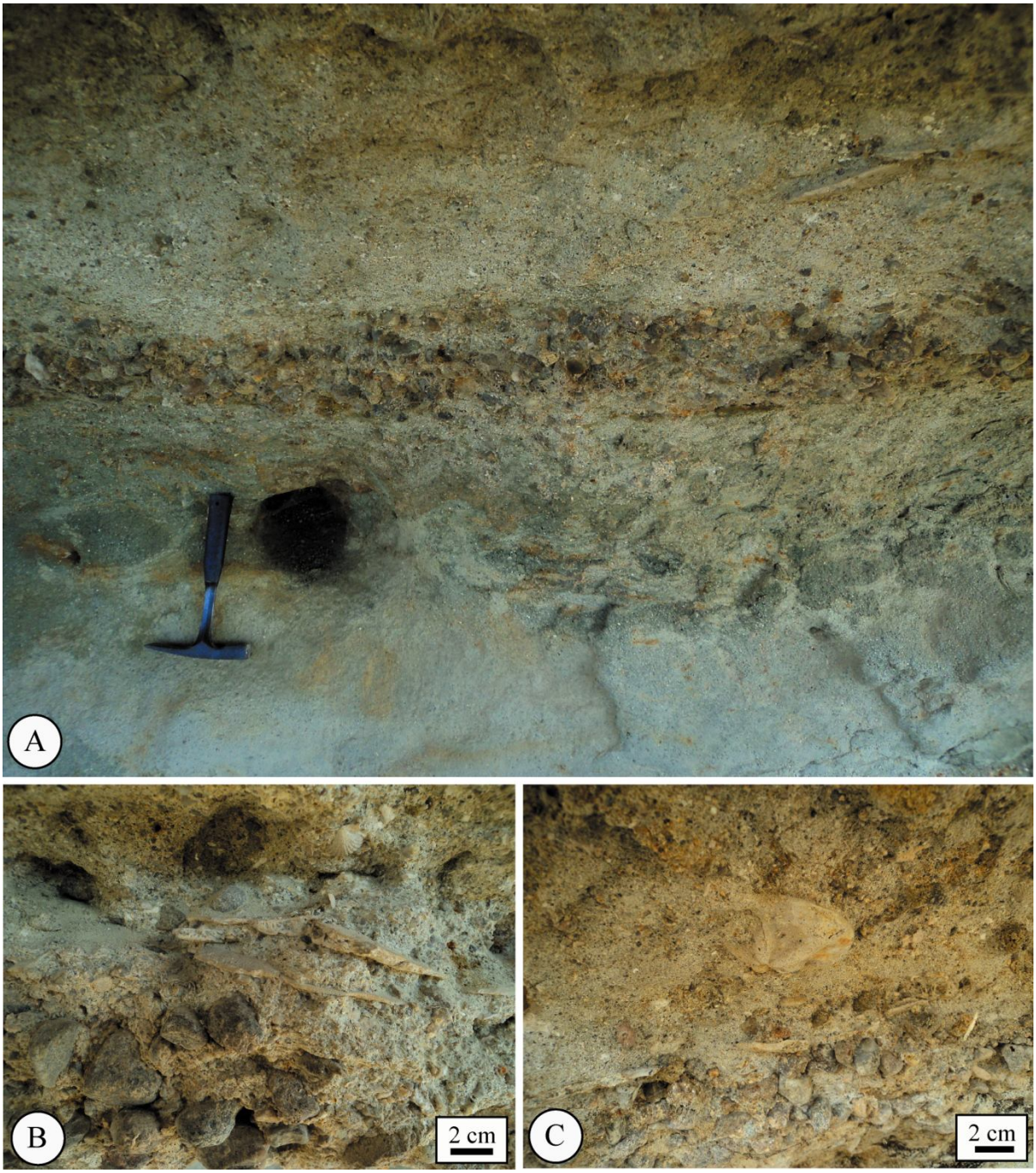

Figure 33. Ardara : A) Detail of the Ardara section showing the clypeasteroid mass accumulation bed (Facies C and D); B) *Amphiope* remains within the conglomerate deposits (Facies C); C) Sand dollar and *Clypeaster* remains within the very coarse sandstone facies above the conglomerates.

4.6. Taphonomy

Features affecting the preservation of the test can be subdivided into those which affect the test before the death of the animal such as sublethal predation, biostratinomic features affecting the skeleton on the sediment surface (abrasion, disarticulation, fragmentation) and those affecting the skeleton after final burial in the sediment including diagenesis. Features related to sublethal predation, disarticulation and radial cracking found in different sections are mentioned below. Other characteristics including orientation data are discussed separately for the different sections.

The tests, especially of *Amphiope*, show various degrees of disarticulation which can be summarized as follows (see Fig. 34A-E).

1) Fully articulated specimens (Fig. 35A).
2) Articulated specimens, but lacking the madreporite.
3) Articulated specimens missing the apical portion of test.
4) Disarticulated specimens lacking the large pie-shaped portions of test with disarticulation occuring along the perradial suture of the ambulacra and poriferous zone of the petals.
5) Sub-triangular test fragments consisting of a high number of articulated plates.
6) Fragments consisting of a small number of articulated plates.
7) Broken specimens

This constitutes a taphonomic gradient from well preserved specimens (though without spines) to highly fragmented material. Taxonomic identification of fragments at generic level in mass accumulations containing both *Amphiope* and *Parascutella* is possible not only because of the presence of the lunules in *Amphiope* (if posterior parts of the test are preserved) but also because of the less robust test with thinner test margins of this genus. Post-burial features include grain indentation, in situ fragmentation or cracking and collapse of the central area of the test. Radial cracking of the test can be quite

common. The cracking occurs along the plate boundaries and follow perradial suture of the ambulacra and poriferous zone of the petals (Fig. 34F). Both complete tests as well as tests lacking pie-shape portions show cracking.

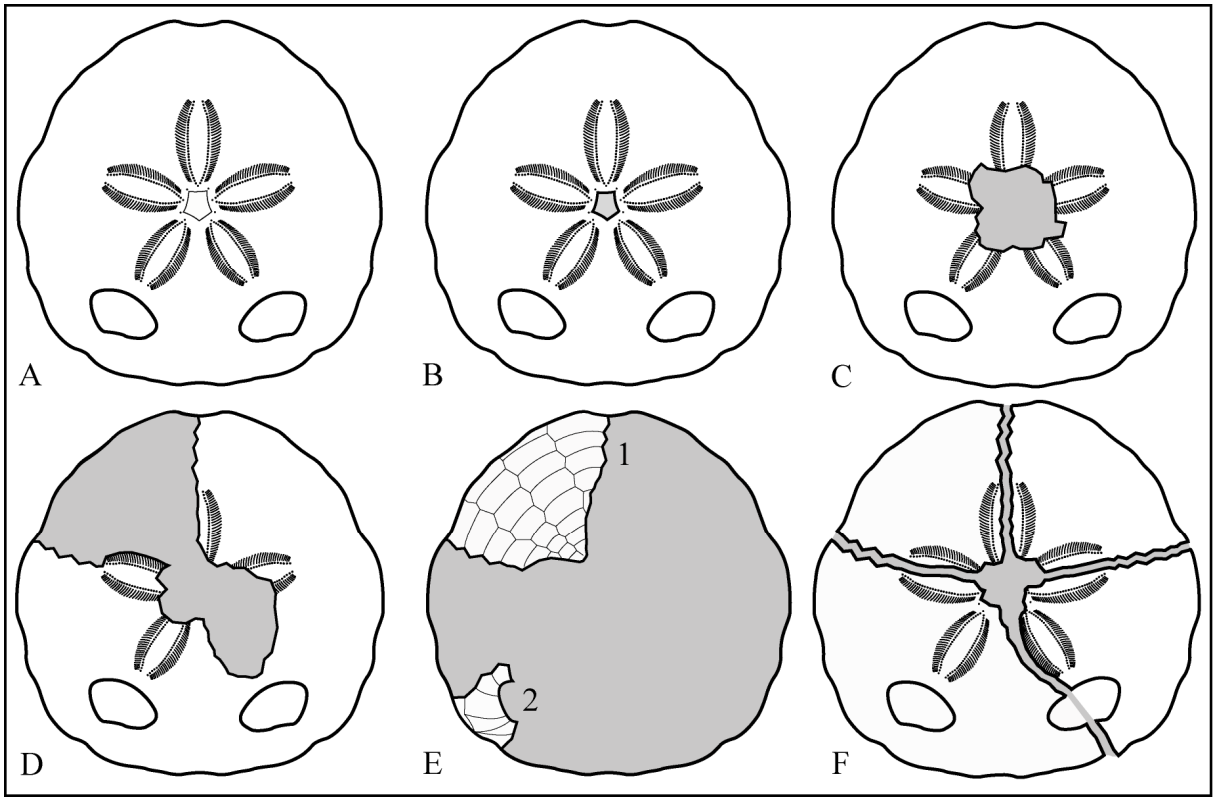

Figure 34. A-E) Disarticulation states of *Amphiope* specimens of Cuccuru Tuvullao. A) Complete specimens (fully articulated specimens); B) Articulated specimens lacking the madreporite; C) Articulated specimens lacking of the apical portion of the test; D) Disarticulated specimens lacking of wide pie-shape portions of the test; E) 1) Sub-triangular pie-shape test fragments and 2) small fragments consisting of an small number of articulated plates. F) Cracked specimens.

4.6.1. Cuccuru Tuvullao (Nuragus)

Clypeasteroids occur in high numbers in the fine to medium, moderately sorted sandstones (Facies B) in the lower part of the measured section. The echinoid deposit is dominated by the genus *Amphiope* (84%) with subordinate *Parascutella* (16%) (Fig. 39A). The echinoid fauna consists exclusively of adult sand dollars (Fig. 40A).

All specimens lack spines; 90% of the tests are fragmented to various degrees (Fig. 39B). Specimens are variously oriented both in plan and cross section. Complete tests are parallel to the bedding plane, both oral side down (75% in life position - Fig. 39C) and oral side up. Complete specimens positioned vertically rarely occur. Test fragment orientations also vary strongly with larger fragments lying parallel to bedding while smaller fragments lie mostly oblique or perpendicular to the bedding plane. The echinoid remains are randomly and homogeneously distributed within the beds and do not form dense aggregations. The tests show various degrees of abrasion, with well-preserved surface specimens mixed with significantly abraded specimens. There is no evidence of encrustation or bioerosion. A wide range of repaired damages to the ambitus of *Amphiope* tests were observed (Fig. 35C, D) and several specimens show radial cracking of the corona (Fig 35B).

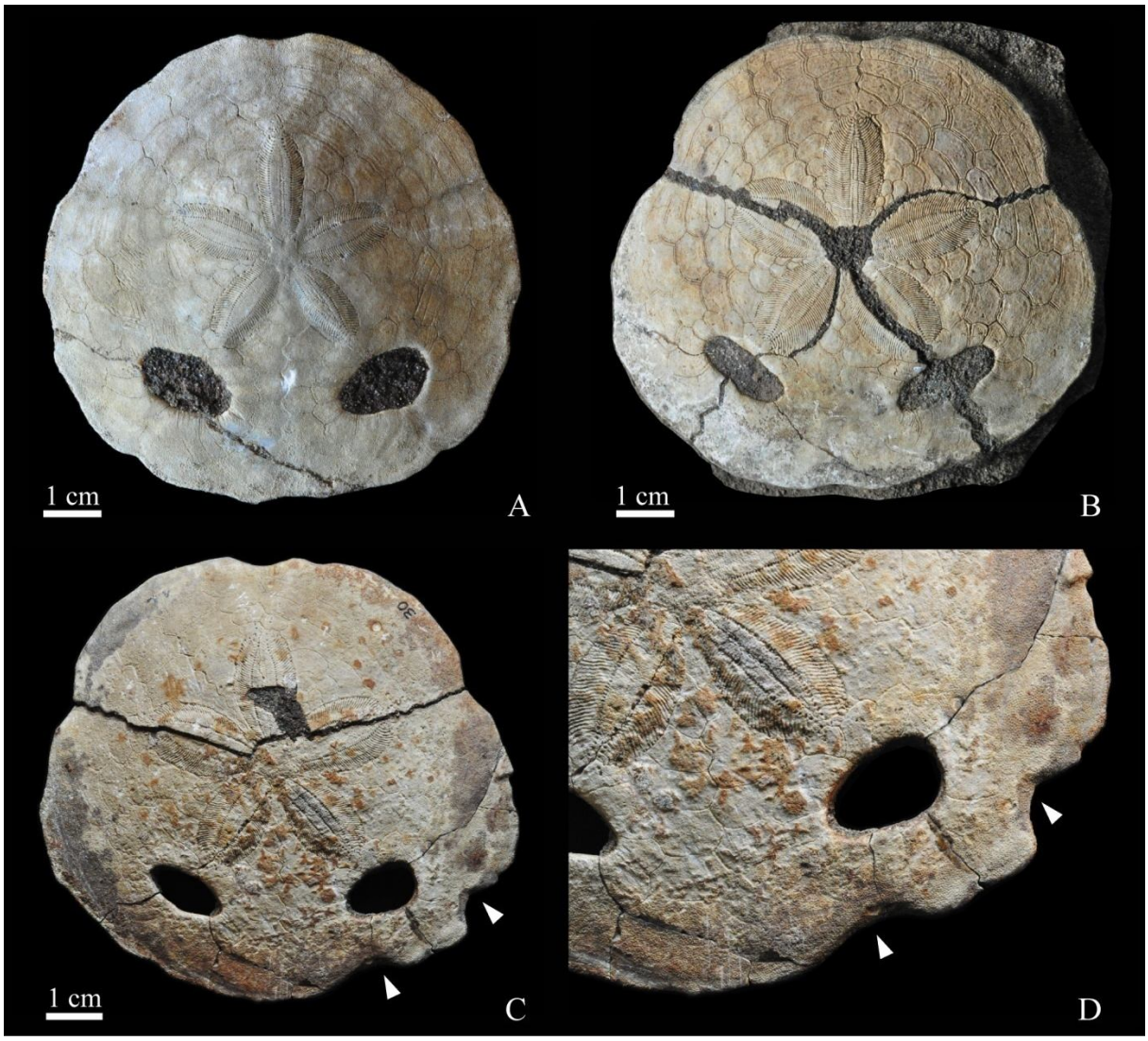

Figure 35. Preservation of sand dollar remains at Cuccuru Tuvullao: A) *Amphiope* complete test (MDLCA23516); B) Cracked specimen (MDLCA23517); C) Evidence of predation on *Amphiope*; D) Detail of the picture C.

4.6.2. Duidduru (Genoni)

The studied fossil assemblage occurs within facies B of the Duidduru section. The fossil assemblage is dominated by the genus *Parascutella* (71%), with subordinate *Clypeaster* (14%) and bivalves (15%) (Fig. 39D).The echinoid fauna consists exclusively of adult sand dollars (Fig. 40B).

The clypeasteroids occur in the middle part of the facies B and form a distinct, 25 cm-thick bed (Fig. 29A, B). The echinoid remains, all lacking spines, include complete test (54%) and variously sized test fragments (46%) (Fig. 36A, B; Fig. 39E). These test fragments range from those representing up to half of the skeleton, to pie-shaped portions of the test to very small fragments. The density of complete tests reaches 70 individuals per m^2. Echinoid test and fragments are loosely to densely packed (*sensu* Kidwell and Holland, 1991). Tests are frequently imbricated.

The echinoids are chaotically distributed both in plan view and in cross section. Measurements of dip direction indicate a dominant orientation between 20° and 70°N (Fig. 41A).The complete specimens show various orientations ranging from concordant to oblique. More than half of the tests (51.4%) are inclined between 30° and 90° (Fig. 41D) as is also reflected by the pole orientation and contour plot (Fig. 41B, C). The tests are mostly oriented oral side down (75.8%) (Fig. 39F).

The surface of the tests is usually very well preserved and surface features such as tuberculation can be readily observed. There is no evidence of predation or bioerosion. A single *Parascutella* specimen was found encrusted by barnacles. Several specimens show repaired damage to the ambitus and radial cracking of test.

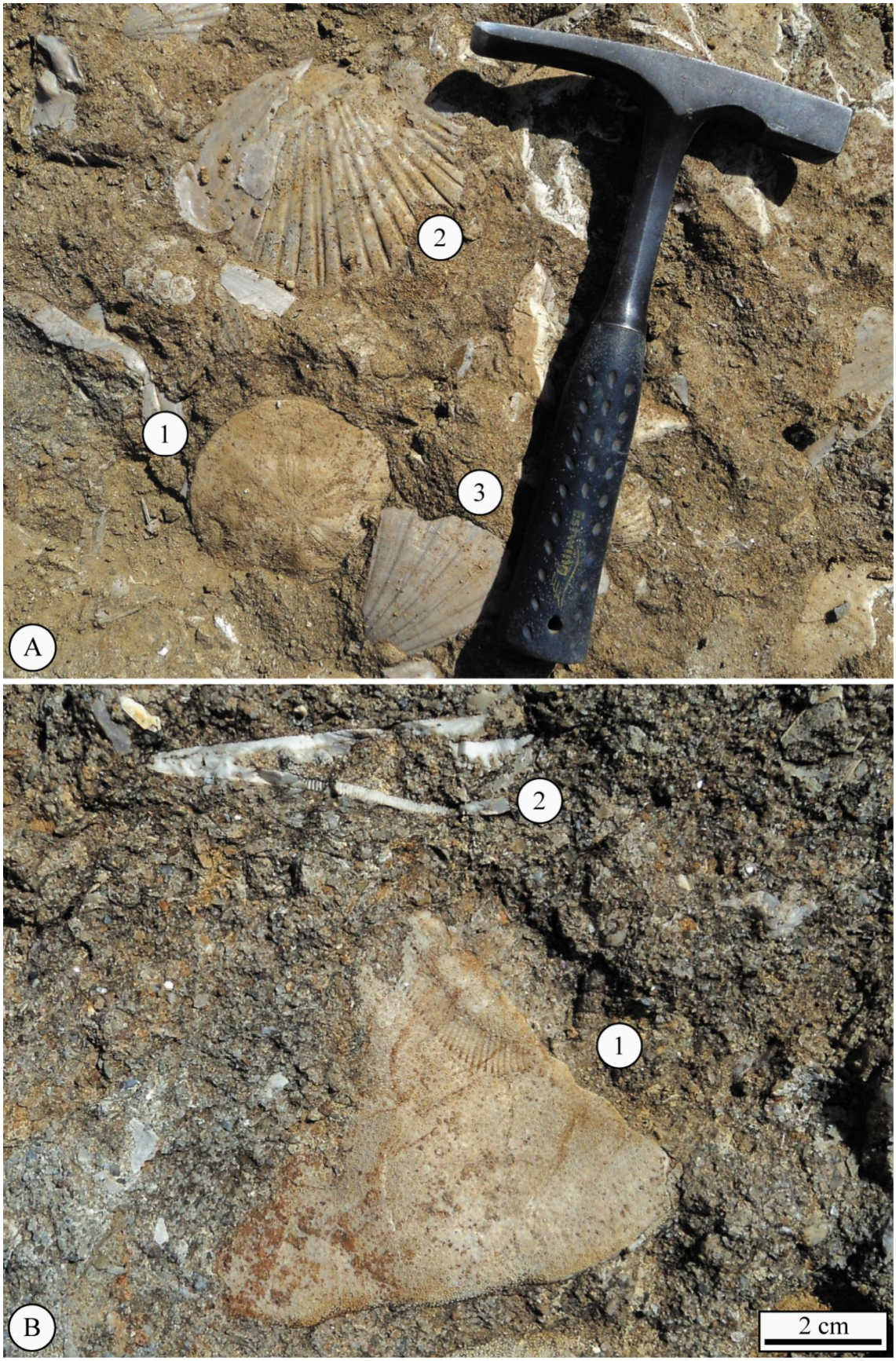

Figure 36. Preservation of fossil remains at Duidduru (Serra Longa Member, Nurallao Formation): A) - 1) Complete test of *Parascutella*, convex up oriented; 2-3) Pectinid remains. B). 1) *Clypeaster* test fragment; 2) *Parascutella* test fragment, convex down

4.6.3. Monte Sa Loca (Chiaramonti)

The mass accumulation occurs in very coarse sands (Facies B) of the lower part of the Monte Sa Loca Section. These beds contain an assemblage of echinoids dominated by the genus *Amphiope* (52%) including both adult and juvenile specimens (Fig. 40C). Other echinoids also occur, including the sand dollar *Parascutella* (6%) and the spatangoid *Agassizia* (42%) (Fig. 39G).

The sand dollars form a distinct, 60 cm-thick layer. This layer is characterized almost exclusively by complete tests (80%) with subordinate fragmented tests (Figs. 37 and 39H). The sand dollars are very densely packed with more than 100 individuals per m^2. The overlapping specimens, however, do not lie in direct contact with one another and are separated by a 0.5 to 1 cm thick sediment layer between the specimens (Fig. 31B). Imbricated specimens are thus not present.

The echinoids are randomly oriented in plan view as denoted by the measurement of dip direction (Fig. 41E). The cross section of the echinoid bed shows that the complete tests range from subconcordant to concordant to the bedding plane (Fig. 31B; Fig. 41H). Oral side up orientations dominate (68% of 50 tests in a cross section area of 30 cm x 160 cm) (Fig.39I). Most of the tests (85.7%) are slightly inclined (Fig. 41F, G).

The specimens do not show evidence of encrustation, boring and predation. Well preserved tuberculation can be observed on those areas of the test surface which are not affected by grain indentation. Specimens often show collapsed central areas of the test (Fig. 37-1).

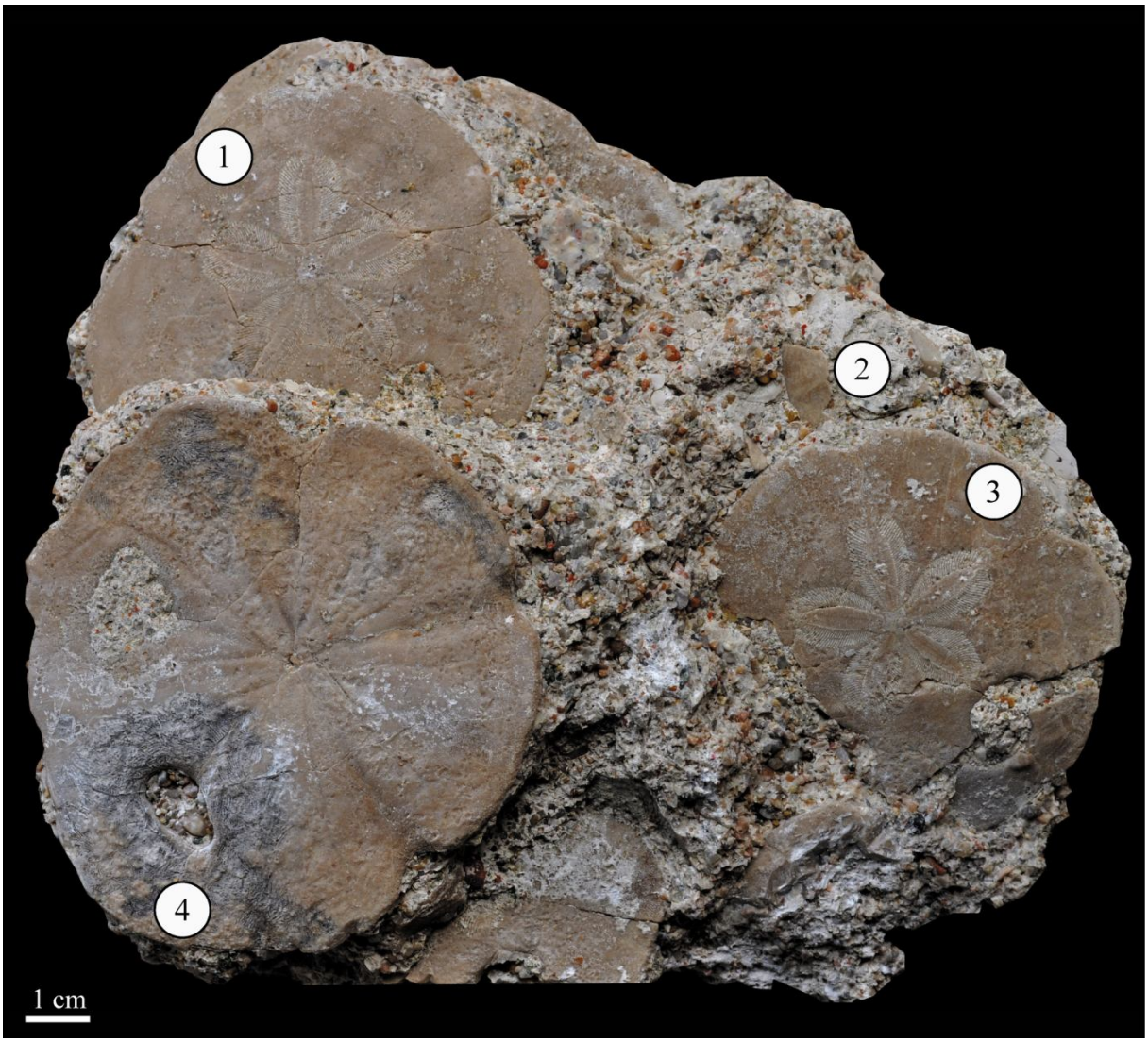

Figure 37. Sample showing the preservation of *Amphiope* remains at Monte Sa Loca (MDLCA23518): 1) Complete specimen showing the collapse of the central area of the test; 2) Test fragment; 4) Broken test; 4) Complete test oriented convex down.

4.6.4. Ardara

The clypeasteroid mass accumulation occurs both in the conglomerate and very coarse sandstone facies of the middle part of the Ardara section. These beds contain an assemblage of echinoids characterized by the genus *Amphiope* (38%) and *Clypeaster* (32%), pectinid remains (30%) and reworked barnacles (Fig. 39L). *Parascutella* very rarely occurs.

The clypeasteroid form a distinct, 100 cm-thick layer. The echinoid remains, all lacking spines, include complete test (58%) and variously sized test fragments (42%) (Fig. 39M and 38A-D). Observation in plan view show that the echinoid remains are not homogeneously distributed. The sand dollar range from very densely to loosely packed and can reached a density of 15 individuals per m^2 while the *Clypeaster* specimens do not lie in direct contact with one another and reached a density of 7 individuals per m^2. Imbricated specimens are not present.

The echinoids are randomly oriented both in plan view and cross section (Fig. 39N). The cross section of the echinoid bed shows that the complete tests range from subconcordant to concordant to the bedding plane. Difference in the dorsoventral orientation of *Amphiope* and *Clypeaster* were observed (Fig. 42).

The sand dollars are mainly convex-up (52,8%) and concordant oriented (66,6%) while the *Clypeaster* are mainly convex-down (51,5%) and oblique or perpendicular oriented (58,2%) (Fig. 42). The specimens do not show evidence of encrustation, boring and predation. The fossil remains show different degree of abrasion. Some fragment show abraded surfaces while in the complete specimens well preserved tuberculation can be observed on those areas of the test surface which are not affected by grain indentation. Some specimens show collapsed central areas of the test and radial cracking.

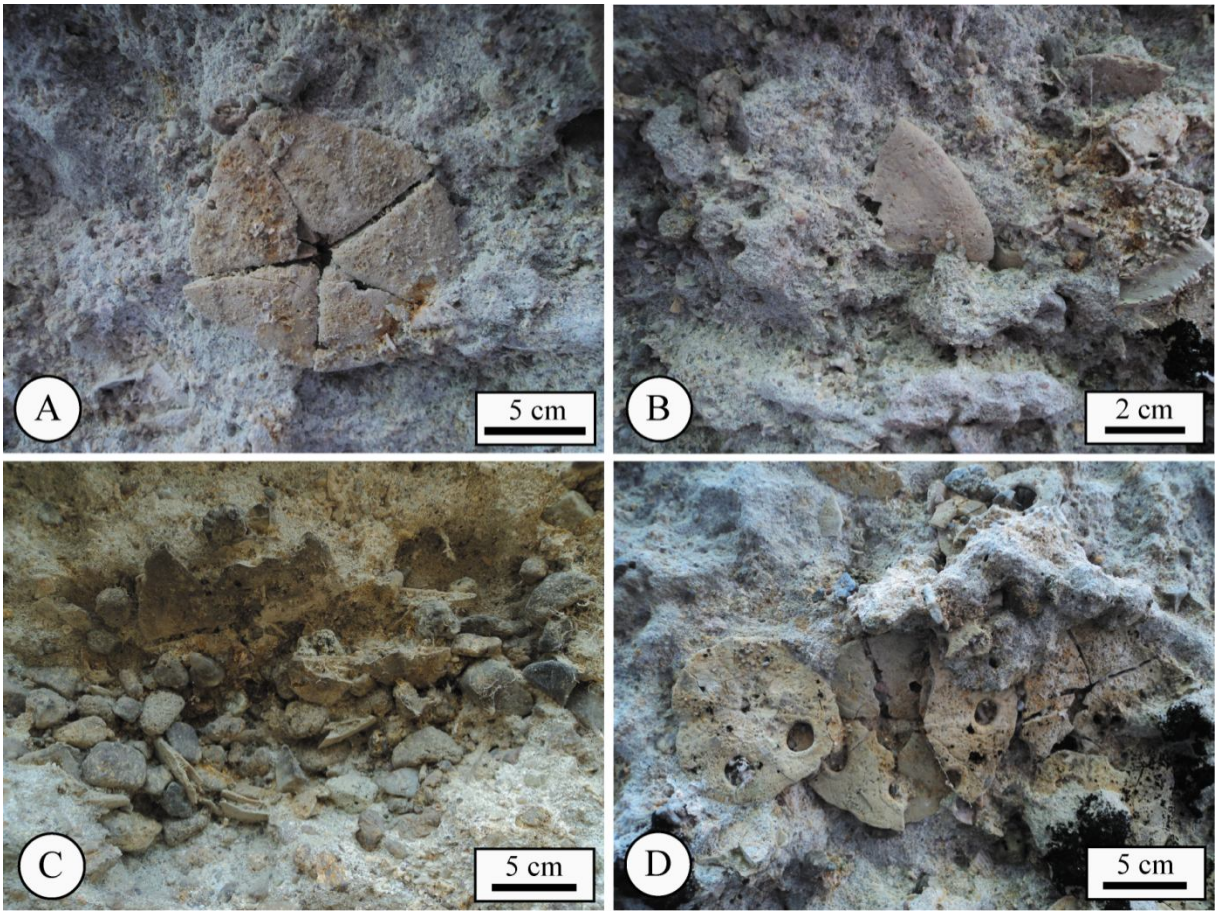

Figure 38. Preservation of clypeasteroid remains of Ardara. A) Complete *Clypeasters* specimens showing radial cracking. B) *Clypeaster* fragment. C) Sand dollar remains whithin the conglomerate deposit. D) Complete specimens and fragments of *Amphiope*.

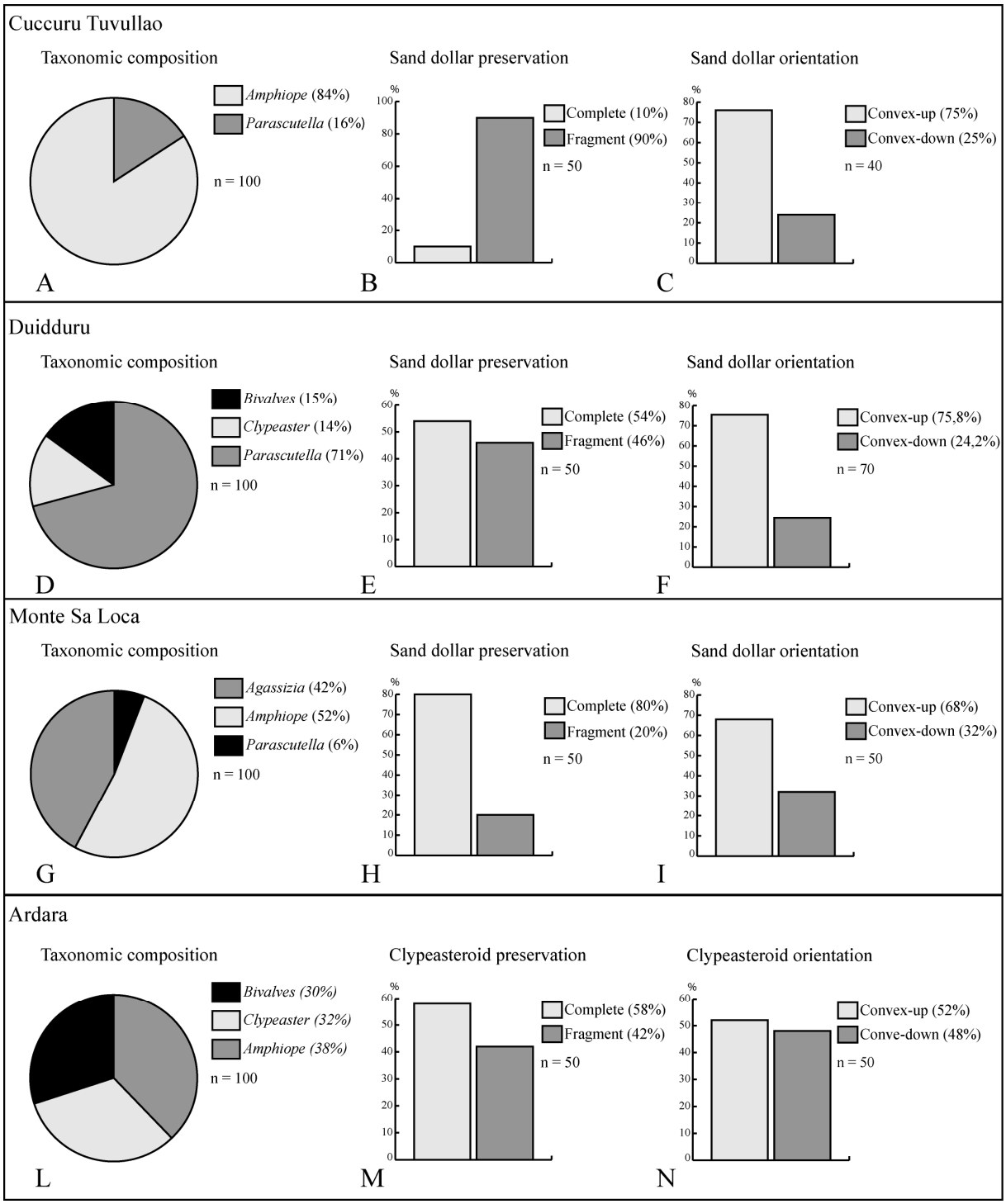

Figure 39. Graphic summarizing the taxonomic and taphonomic data of Cuccuru Tuvullao, Duidduru, Monte Sa Loca and Ardara clypeasteroid assemblages. A; D; G; L) Taxonomic composition; B; E; H; M) Bar diagram showing the percentage and the number of sand dollar remains (fragments and complete test); C; F; I; N) Bar diagram showing the dorsoventral orientation of complete test; n indicates the number of specimens.

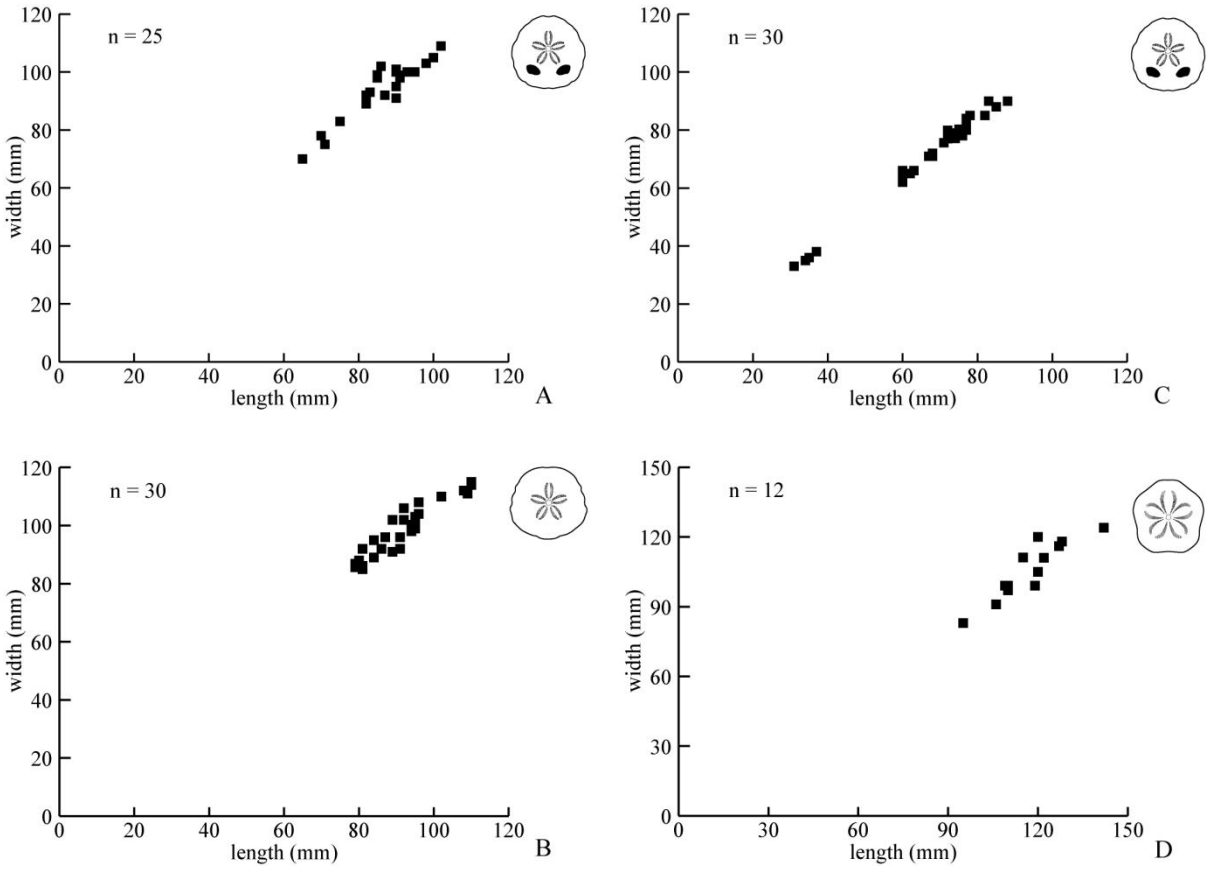

Figure 40. Scatter diagram of test length vs. test width. A) Cuccuru Tuvullao assemblage; B) Duidduru assemblage; C) Chiaramonti assemblage; D) *Clypeaster* specimens in the Ardara assemblage. n indicates the number of specimens.

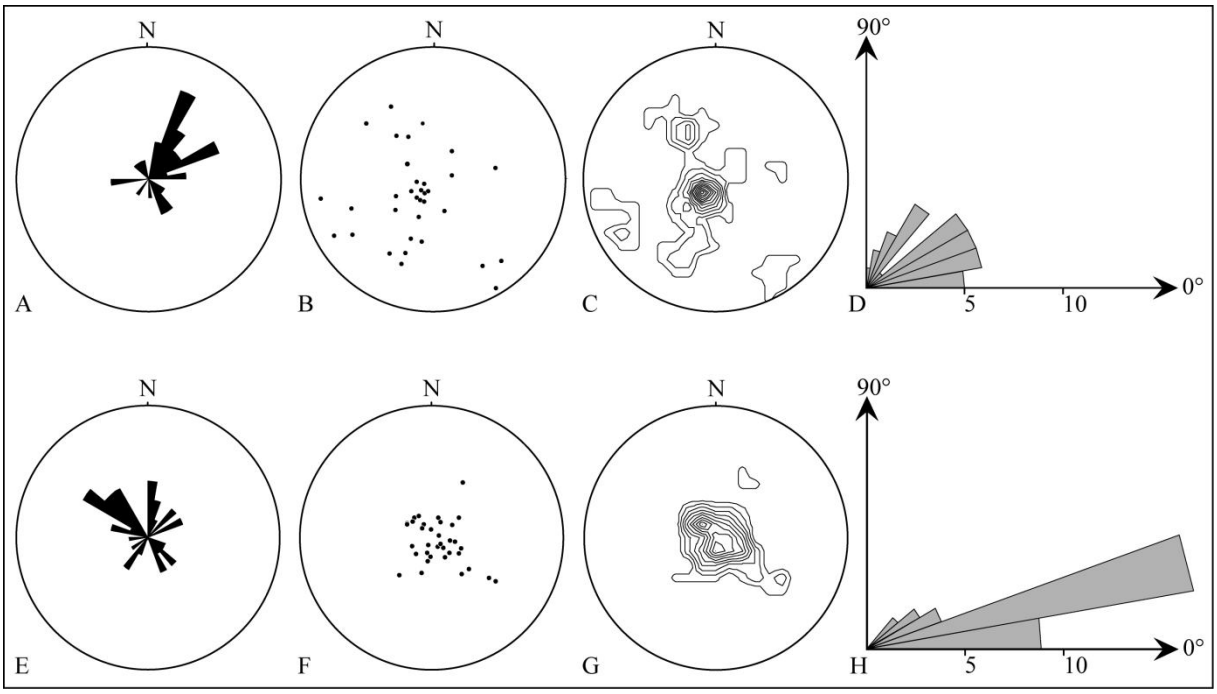

Figure 41. Directional data of Duidduru (A, B, C, D) and Monte Sa Loca (E, F, G, H) sand dollar assemblages. A, E - Rose diagram of dip direction in 10° classes. B, F -Pole axis distribution (Stereonet 7, equal area projection, lower hemisphere). C, G - Pole axis contour plots (Stereonet 7, equal area projection, lower hemisphere). D, H – Dip angle in 10° classes.

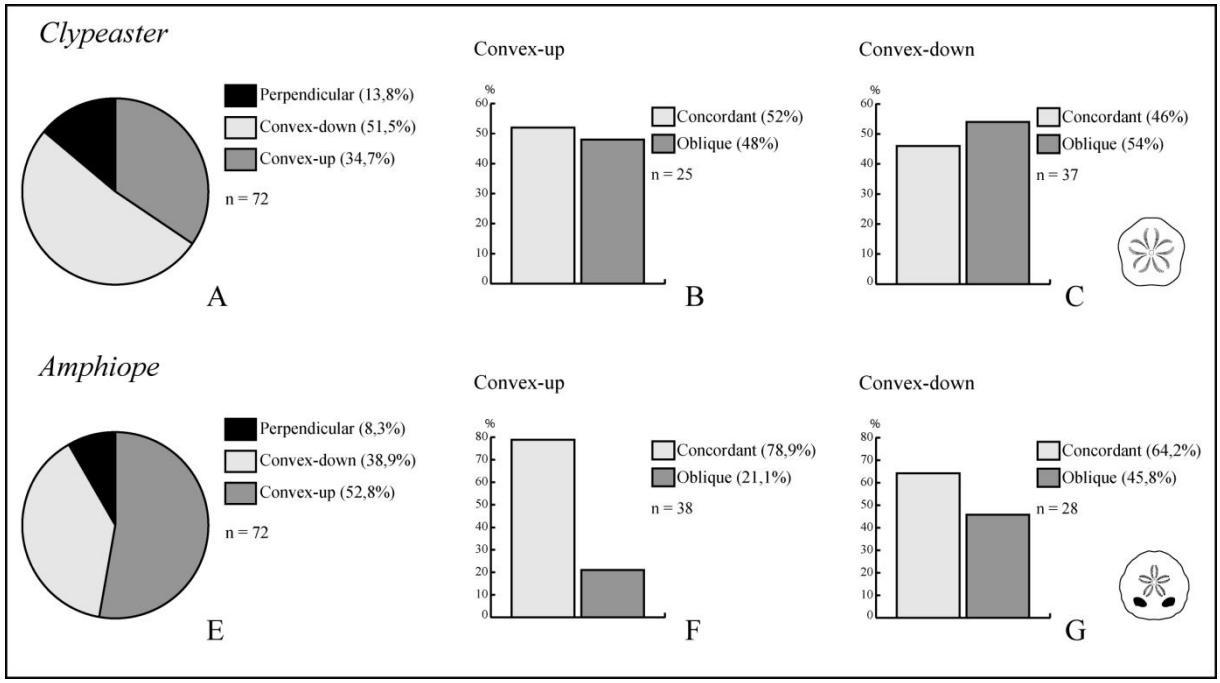

Figure 42. Orientation data of Ardara clypeasteroid assemblage: A, B, C) *Clypeaster*; E,F,G) *Amphiope*. n indicates the number of counted specimens.

4.7. Discussion

4.7.1. Origin of sand dollar accumulations and palaeoenvironmental inferences

As discussed by Nebelsick and Kroh (2002), the genesis of sand dollar accumulations can be related to four mechanisms: 1) obrution; 2) in situ reworking; 3) subtidal accumulation, and 4) supratidal accumulation. Each of these processes should leave different sedimentological and taphonomic signatures potentially allowing for the origin of these deposits to be inferred. Although the studied sand dollar assemblages show differences, some common features were recognized. The sections consist of clastic sequences whose sedimentological and palaeontological features point to shallow water, shoreface environment. The preservation of clypeasteroid tests and the origin of mass accumulations in sandy bottom shoreface environment can be promoted by sediment movements, rapid burial and physical concentration of skeletal material through transport, winnowing, reworking or amalgamation.

4.7.2. Palaeoecology of the fossil clypeasteroid echinoids

Amphiope and *Parascutella* show a very flat profile and lack some of the morphological features such as the eccentricity of the apical system and the food grooves extending to the apical side of the test, which are commonly associated to suspension feeding forms, such as *Dendraster excentricus* (Fig. 43D). Although these morphological features do not exclude vertical posture and suspension feeding strategy, as denoted by Lawrence et al. (2004) for *Encope michelini*, an interpretation of *Amphiope* and *Parascutella* as shallow burrower, deposit feeding forms, like *Echinodiscus*, *Mellita* and *Encope*, is proposed (Fig. 43 C).

Living species of the deposit feeding genus *Clypeaster* widely differ in shape and behaviour (Telford et al., 1987). Those species with flat profiles, thin margin and flat ventral surface are commonly associated to shallowly buried or semi-infaunal lifestyles

as shown by such forms as *Clypeaster subdepressus* (Fig. 43A). *Clypeaster* species with the high test profiles, thick margins and the oral surfaces with large and deep infundibulum are typical for epibenthic forms such as *Clypeaster rosaceous* (Fig. 43B). By analogy with recent species, the analysis of functional morphology and the occurrence in the fossil record Rose and Poddubiuk (1987) believe that morphological variation of *Clypeaster* through time, from small and very depressed to high inflated form, could reflect an expansion of the ecological range of the genus with varied and surface-dwelling strategies. *Clypeaster* specimens of the Duidduru assemblage have moderately high test profiles, relatively thick and tumid margin and a flat ventral surface with a small infundibulum. These *Clypeaster* seems to represent an intermediate form between the *Clypeaster subdepressus* and *Clypeaster rosaceous* morphotypes and can, therefore, be interpreted as partially burrowed, deposit feeders.

The *Clypeaster* specimens of Ardara show a great heterogeneity of form as concern test size, ambital outline, profile, shape of petals etc.. The presence of different *Clypeaster* morphologies (morphotypes) suggests an environment where different food resource were utilised. The specimens with very flat test profile and thin margins are interpreted as burrowing deposit feeders while the well shaped form with thick and tumid margins and large infundibulum are interpreted as epibenthic deposit feeders. A third intermediate form with elevated petals could be interpreted as partially burrowed deposit feeders.

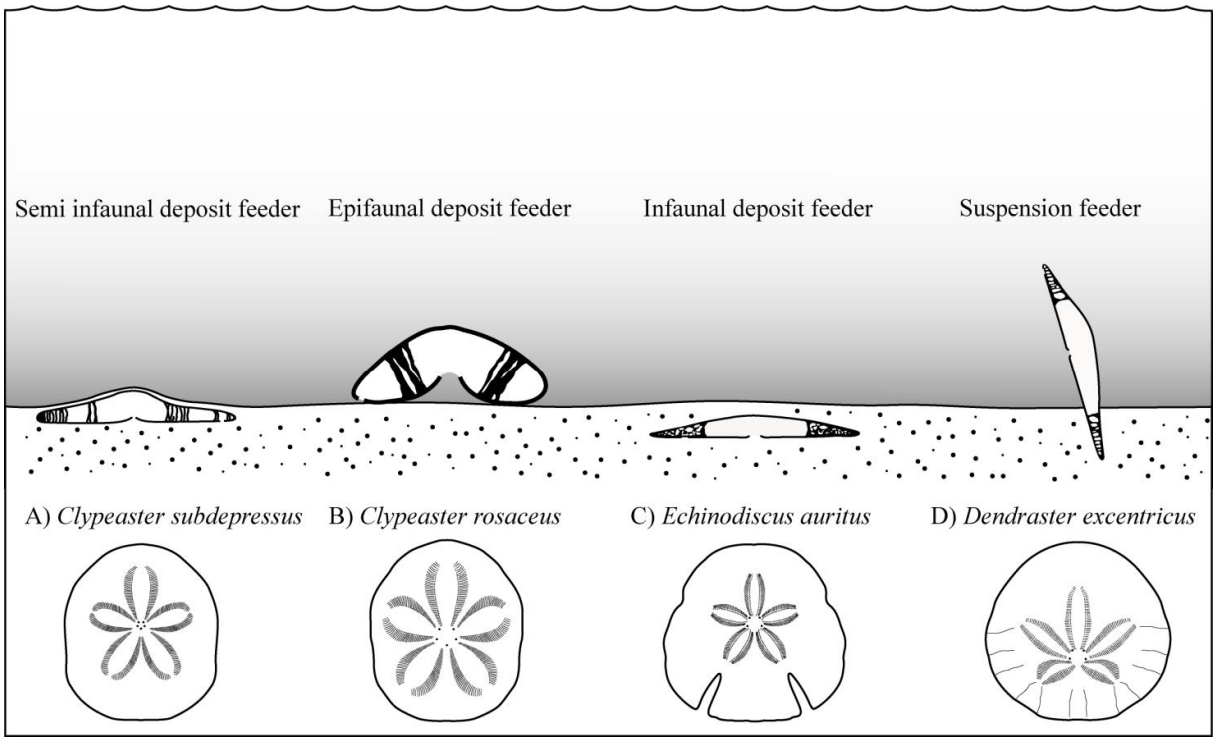

Figure 43. Clypeasteroid are a group of echinoids which adopt different feeding strategy from shallow burrowing, such as *Clypeaster subdepressus* (A) and *Echinodiscus auritus* (C) *to* epibenthic, such as *Clypeaster rosaceous* (B) (Telford et al., 1987). The sand dollar *Dendraster excentricus* has the ability to feed either on deposited or suspended food particles (Fodrie et al., 2007).

4.7.3. Transport and orientation

The sand dollar tests, with their thin discoidal shape, slightly domed aboral surface and flat or slightly concave oral surface could be subjected to hydrodynamic lift in a water current (Chia, 1973; Telford, 1981) and thus be readily transported. Hydrodynamic experiments conducted by Telford (1981) on the lunulate sand dollar *Mellita* and non-lunulate *Echinarachnius* show that the presence of lunules reduces this lift effect. Experiments on *Mellita* shows that the lifting velocities can vary from 40 to 90 cm s^{-1} for test sizes from 1 to 9 cm respectively, while *Echinarachnius* specimens of similar size has a lifting velocity of 22 and 77 cm s^{-1}. More studies are needed to determine the reactions of different sand dollar morphologies to flow velocities, but these results suggest that: 1) the lunulate sand dollars can tolerate higher energy environment than those without and that 2) as intuitively expected smaller specimens of a given genus can be more easily transported than larger specimens. The occurrence of both juvenile and adult sand dollars in the Chiaramonti assemblage may suggest lower flow velocities to be reconstructed than in the other localities. The fabric of the three studied sand dollar deposits markedly differs; the complete specimens and large fragments of Cuccuru Tuvullao and Chiaramonti show mostly aboral side up orientation (convex up orientation), while the sand dollars of Duidduru and Ardara are chaotically arranged. Concordant, convex up orientations denote a stable hydrodynamic position under lower transport velocities, while irregular orientations of specimens imply higher transport velocities.

The different orientation of *Amphiope* and *Clypeaster* test in the Ardara assemblage could be induced to different hydrodynamic behaviour related to dissimilar test shape between these genera.

4.7.4. Predation

Evidence of non-lethal predation on the sand dollar test is common here. Echinoids are predated by a different organism such as gastropods, crabs, fishes, turtles, and other echinoderms (Nebelsick, 1999; Kowalewski and Nebelsick, 2003). Recognisable traces on the test, which range from drill holes to irregularities of the ambitus, resulting from predation can be recognized. Some specimens of *Amphiope* and *Parascutella* of Cuccuru Tuvullao and Duidduru show both semi-circular and irregular repaired test indentations (Fig. 14C, D). These damages are interpreted as test scars related to non-lethal predator activity. Similar test damages are documented for both living sand dollar, such as *Echinodiscus* and *Encope* (Nebelsick and Kampfer, 1994; Kier and Grant, 1965) and fossil ones (such as *Monophoraster* and *Parascutella*) (Zinsmeister, 1980; Nebelsick, 1999) and are presumably related to predation from crabs or fish.

4.7.5. Disarticulation

The degree of disarticulation of an echinoid test depends on many factors including the amount of skeletal strengthening between individual plates and the rates of decay of connective tissues (Allison 1990, Kidwell and Baumiller, 1990). Experiments carried out by Nebelsick and Kampfer (1994) on *Echinodiscus auritus* reveal that plate disarticulation occurs rapidly (1 day) once the test is broken. Taphonomic observations denoted that the sand dollar remains, which always lack their minute spines, frequently occur as fragments, particularly in the Cuccuru Tuvullao, Duidduru and Ardara assemblages (Fig. 12B, E). This high percentage of fragments suggests that the sand dollars have undergone repeated agitation leading to test fragmentation.

4.7.6. Encrustation and bioerosion

Encrustation as a taphonomic proxy can potentially be used to provide a measure of the duration of post-mortem exposure of shells on the sea floor (see Beckvar and Kidwell, 1988). Colonization by encrusting organisms can occur in relatively short time, from weeks to months, in shallow marine environments (e.g. Sutherland and Karlson, 1977; Nebelsick et al., 1997).

As discussed by Nebelsick et al. (1997), Santos and Mayoral (2008) and Belaùstegui et al. (in press) cassiduloids and clypeasteroids with their high preservation potential can potentially offer favourable substrates for skeletozoan colonization in sandy shoreface environments (Fig. 44). Especially *Clypeaster* and *Echinolampas* with its large and rather sturdy tests, have the potential to form benthic islands (sensu Seilacher, 1982) which can be frequently encrusted and bioeroded.

Although barnacles are found in the Cuccuru Tuvullao, Duidduru and Ardara clypeasteroid deposits, both on encrusting large pebbles and as reworked fragments, echinoid tests do not show evidence of encrustation.

The general lack of encrustation of the echinoids in the studied localities suggest a short residence time of the skeletons on the sea floor but could also reflect the more frequent mobilization of the remains than the large heavy pebbles which do show encrustation.

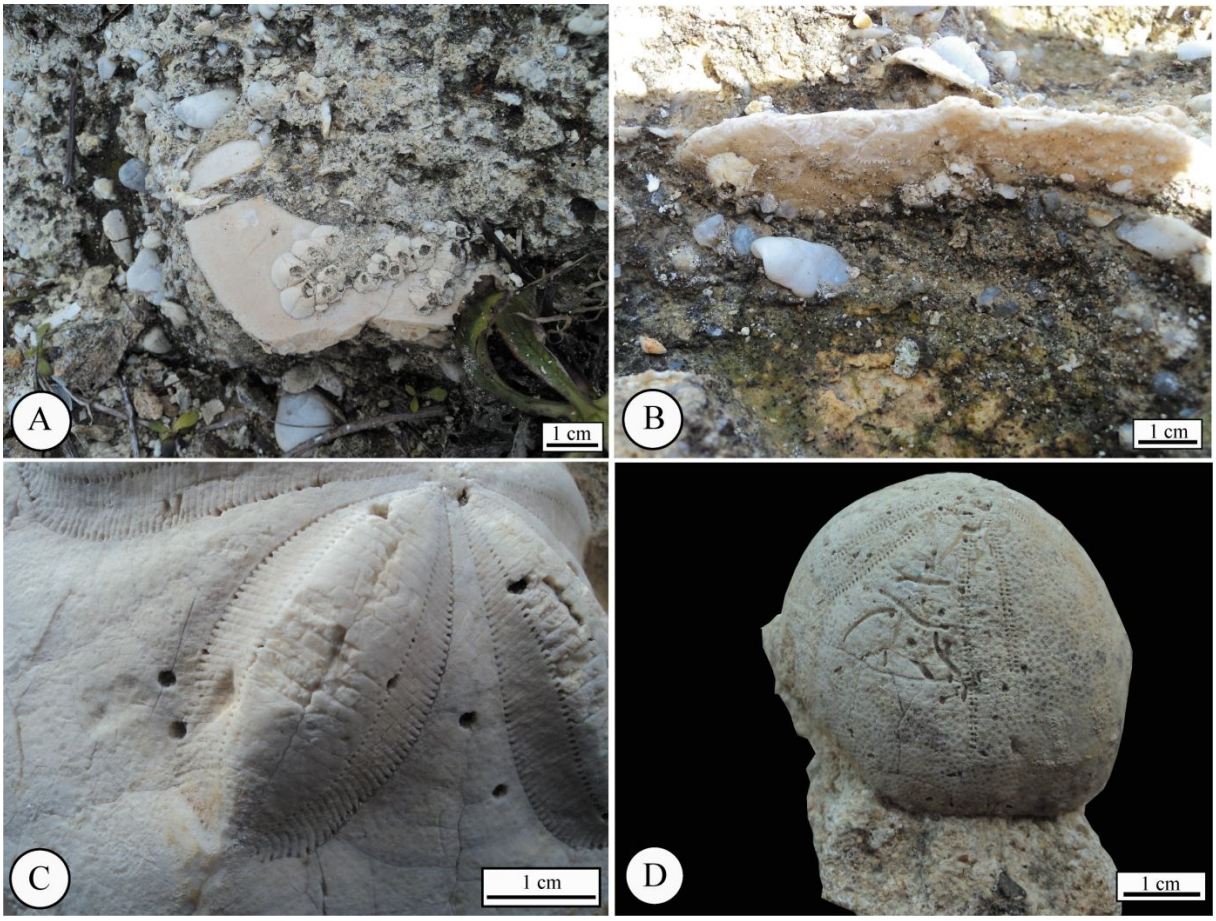

Figure 44. Encrustation and bioerosion on echinoid tests. A-B) Encrustation on *Amphiope* test from Bancali (SS); C) Bioerosion on *Clypeaster* test (Pozzomaggiore); Encrustation by serpulid worms on *Echinolampas* from Cuccuru Tuvullao (Nuragus).

4.7.7. Post-depositional features

Some specimens are affected by symmetrical fragmentation along the perradial suture of the ambulacra and poriferous zone of petals (Fig. 14B). As discussed by Nebelsick (1999) upon comparison between recent and fossil sand dollars, the symmetrical fragmentation that occurs in some specimens represents post burial radial cracking resulting from sediment loading. The clypeasteroid tests are usually affected by grain indentation, a post-burial processes which can reduce the possibility to recognize important features of the surface.

4.8. Interpretation of different mass accumulations

4.8.1. Cuccuru Tuvullao

In the measured section, the sand dollar remains occur in a medium-coarse, poorly sorted, sandstones (Facies B), located between a conglomerate deposit (Facies A) and a very fine sandy facies, characterized by the high abundance of *Turritella* (Facies C). In agreement with Sowerbutts and Underhill (1998), the conglomerates are interpreted as deltaic marine deposits, as shown by the sedimentary structures and the fossil content. Facies C is a turritellid-dominated assemblage deposit (sensu Allmon, 2007). *Turritella* is a semi-infaunal, suspension feeding gastropods which commonly inhabit shallow waters sandy and muddy facies (Giacobbe and Mondello, 1994; Allmon, 2011). The Lower Miocene clastic sequence in the Cuccuru Tuvullao area thus documents the transition from deltaic deposits of the Conglomerato di Duidduru Member to littoral marine deposits of the Arenarie di Serra Longa Member and denotes a retrogradation of very shallow-water facies.

The sand dollar deposit which is dominated by *Amphiope* is matrix-supported with the fossils dispersed within the sediments. A multiple in situ physical reworking origin is suggested due to the differential orientation of complete tests, which are preferentially concordant to the bedding plane and prevalently convex up. The general situation may be similar to that described by Salsman and Tolbert (1965) for the living sand dollar *Mellita quinquiesperforata* from the near shore environment of the Gulf of Mexico. These sand dollars formed very dense aggregation which underwent episodes of mass mortality followed by breakage of sand dollar tests, though. Repeated high energy periods lead to high abrasion and fragmentation as well as orientation of larger specimens occurred. The origin of the Cuccuru Tuvullao sand dollar accumulation is due to an interplay of multiple episodes of reworking, presumably related to storms and fair weather wave actions, and low sedimentation rates within a retrogradational phase.

Although the sandstone deposit shows a massive aspect without evidence of internal stratification, the alignment of large rounded pebbles and cobbles at middle levels of this poorly sorted sandy facies could be related to the capacity of storm to generate lags, as described by Kumar and Sanders (1976), Hayes (1967) and Kreisa (1981).

4.8.2. Duidduru (Genoni)

This 25 cm-thick layer within a coarse, moderately sorted sandy facies shows a clear predominance of *Parascutella* over *Clypeaster*. The simultaneous presence of sand dollars and *Clypeaster* is not uncommon in the fossil record (Kroh and Nebelsick, 2003, Belaústegui et al., 2012). This sand dollar dominated assemblage consists of both complete specimens and fragments of different sizes and shape. Fragmentation is relatively low compared to the Cuccuru Tuvullao locality. This fact together with low abrasion of the echinoid surface suggests relative short surface residence times which is also supported by the low degree of encrustation and absence of bioerosion. The high frequency of articulated pectinids corroborates this interpretation. The directional transport could be indicated by the dominant orientation of the dip direction. The high percentage of obliquely oriented specimens suggests a transport of the skeletons. On the basis of the taphonomic features, clast relationships, sedimentary fabric and bed morphology, along with the persistence of the internal layer morphology across large distance (hundred meters), the sand dollar dominated assemblage of Duidduru could represent a proximal storm deposits.

4.8.3. Chiaramonti

The sand dollar assemblage occur in coarse, poorly sorted carbonate-cemented sandstones, which in agreement with Funedda et al. (2000) represent both sandy shore bottom and fossiliferous sand bars, probably linked to minor regressive phases in a clear evident transgressive trend. The high proportion of well-preserved tests with a preferentially concordant, convex up orientation suggests the lack of extended physical reworking or transport. This interpretation is corroborated by the presence of juveniles which would be more easily removed by higher currents. Specimens not affected by grain indentation show well preserved tubercles and thus low abrasion rates. The absence of encrustation and bioerosion indicate a permanence of the remains at the water/sediment interface. These features suggest that the sand dollar bed of Monte Sa Loca represent a relative autochthonous assemblage in a lower energy setting than the other sections; the origin of this echinoid bed took place in a minor progradational phase with high sedimentation rates within a more general transgressive trend.

The presence of preserved tests of *Agassizia* corroborates this interpretation. These echinoids were also found in a similar setting in the Miocene locality of Alahan in Turkey (Nebelsick and Kroh, 2002).

4.8.4. Ardara

The clypeasteroid assemblage occurs in massive conglomerate and coarse poorly sorted cemented sandstone. These facies suggest a shallow water high energy environment.

This clypeasteroid mass accumulation consists of both complete specimens and fragments of different sizes and shape. This fact together with low surface abrasion of the complete echinoid specimens suggests a relative short surface residence times as is also supported by the low degree of encrustation and absence of bioerosion. The high percentage of obliquely and perpendicular oriented specimens, particularly as for the *Clypeaster* specimens, suggest a transport of skeletons. On the basis of the taphonomic features, clast relationships, sedimentary fabric and bed morphology, along with the persistence of the internal layer morphology across large distance (hundred meters), the sand dollar dominated assemblage of Duidduru could represent a proximal storm single event.

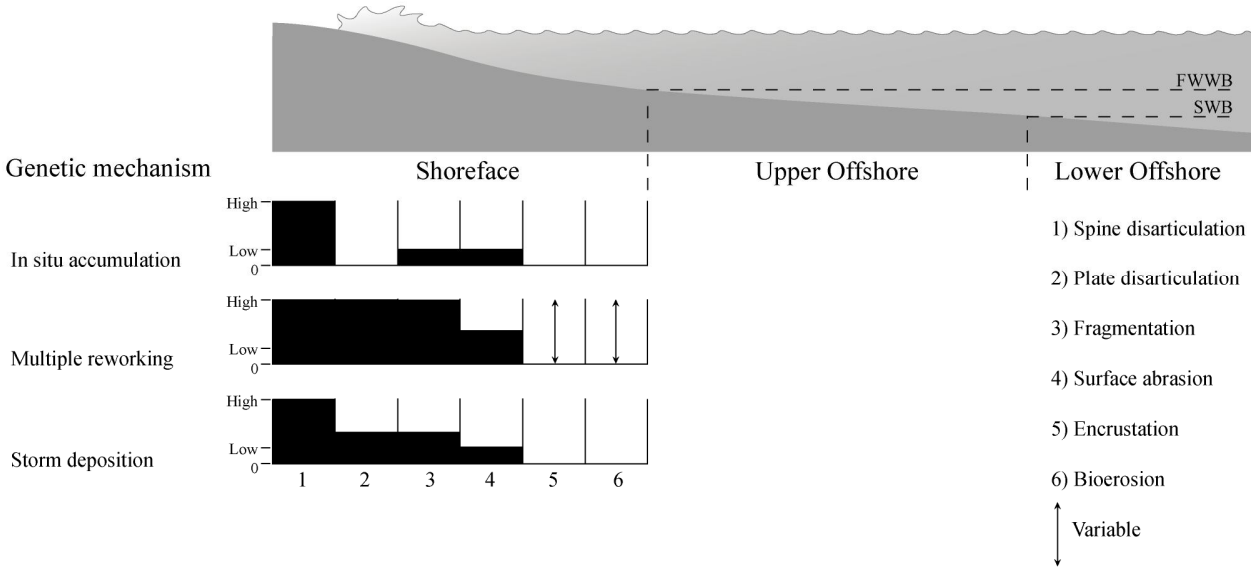

Figure 45. Observed variations in the taphonomic signatures of mass accumulation of clypeasteroid echinoids are due to different genetic mechanisms, which occur in the shoreface environment.

4.9. Conclusions

1) Clypeasteroids, particularly sand dollars, frequently form shell concentrations in the shallow water sediments of the Miocene of Sardinia. In order to infer the origin of four such sand dollar accumulations from the Miocene of Sardinia, detailed taphonomic, stratigraphic and sedimentological analyses were made.
2) Two fossil assemblages are dominated by the genus *Amphiope* with subordinate *Parascutella*, while the other accumulation is dominated by *Parascutella* with subordinate *Clypeaster*. These assemblages thus show a low diversity, as denoted by other sand dollar accumulations in the Neogene of the Mediterranean area.
3) The fossil sand dollar dominated accumulations originate from to a combination of a number of ecological, morphological and sedimentological aspects. The gregarious behaviour, the robust, flat, low density sand dollar test and their habitat in the shoreface environments are the three main factors that lead to these sand dollar deposits.
4) Although all the three studied sand dollar deposits can be assigned to a shoreface environment, there are differences in their features and origin (see Fig. 45 and Table 2). The *Amphiope* deposit of Cuccuru Tuvullao represents an example of a multiple in situ reworking accumulation in a retrogradational phase with low sedimentation rates. The *Parascutella* dominated concentration of Duidduru and Ardara clypeasteroid deposit constitute proximal storm single events. The *Amphiope* dominated bed of Monte Sa Loca represents a relative autochthonous assemblage, presumably related to progradational phase with high sedimentation rates.
5) In spite of the different origin of the sand dollar deposits, a low degree of encrustation and absence of bioerosion of the tests were constantly observed. This pattern could be related to short residence time of the sand dollar tests on the sea

floor, but could be also due to the frequent mobilization of the skeleton remains in high energy environments.

6) Mass accumulations of clypeasteroids, with their widespread distribution and diversification, represent the main contributors to echinoderm shell beds in the Miocene of the Mediterranean area.

Table 2. Summary of taxonomic, sedimentologic and taphonomic features of the three studied sand dollar assemblages from the Lower Miocene of Sardinia. Part 1.

Locality & Stratigraphy				
Locality	Cuccuru Tuvullao	Duidduru	Monte Sa Loca	Ardara
Age	Lower Miocene	Lower Miocene	Lower Miocene	Lower Miocene
Sedimentary environment	Siliciclastic	Siliciclastic	Siliciclastic	Siliciclastic
Thickness of the accumulation	220 cm	25 cm	60 cm	100 cm
Diversity and size variation				
Taxonomic composition				
Clypeaster	0%	14%	0%	32%
Amphiope	84%	0%	52%	38%
Parascutella	16%	71%	6%	0%
Others	Barnacles	Bivalves 15%	*Agassizia* 42%	Bivalves 30%
Age spectrum	Adults	Adults	Juveniles & adults	Adults
Sedimentary fabric				
Density	Randomly dispersed	Densely packed	Densely packed	Densely to loosely packed
Imbrication	Absent	Present	Absent	Present
Orientation of complete specimens				
Concordant	Dominant	Present	Dominant	Present
Oblique	Present	Present	Rare	Present
Perpendicular	Present	Present	Absent	Present
Convex up	75%	76%	68%	52%

Table 2. Summary of taxonomic, sedimentologic and taphonomic features of the three studied sand dollar assemblages from the Lower Miocene of Sardinia. Part 2.

Detailed taphonomy				
Spine disarticulation	Total	Total	Total	Total
Intraplate disarticulation	High	Low	Low	Low
Interplate fragmentation	Low	Low	Low	Low
Surface abrasion	Low to High	Low	Low	Low
Edge rounding	Present	Absent	Absent	Absent
Encrustation	Absent	Rare	Absent	Absent
Predation				
Lethal	Absent	Absent	Absent	Absent
Non-lethal	Present	Present	Absent	Absent
Post depositional features				
Grain indentation	Present	Absent	Present	Present
Radial cracking	Present	Present	Absent	Present
Implosion of the central area of the test	Absent	Absent	Present	Absent
Palaeoenvironment				
Interpreted environment of origin	Shoreface	Shoreface	Shoreface	Shoreface
Interpreted environment of deposition	Shoreface	Shoreface	Shoreface	Shoreface
Genesis of accumulation	Multiple in situ reworking	Proximal Storm deposit	In situ accumulation	Proximal Storm deposit

Chapter 5.

Taphonomy and palaeoecology of regular echinoid and spatangoid mass accumulations from the distal shelf sediments of the Miocene of Sardinia: a window onto the origin of echinoid concentration beds in offshore environments

This chapter integrates stratigraphic, sedimentologic, taphonomic and palaeoecologic data on regular echinoid and spatangoid mass accumulations, which are extremely rare in the fossil record of the Miocene of Sardinia, in order to reconstruct their origin and palaeoecology.

5.1. Regular echinoids

5.1.1. Morphology of regular echinoids

Echinoids were a minor component of the Palaeozoic benthic fauna, as denoted by their poor fossil record in this Era. The origin of modern echinoid fauna can be traced to the Permian with the appearance of the first cidaroids and the ancestors of euechinoids. Diversity increase throughout the Mesozoic with a great radiation during the Jurassic when the major lines of echinoids appeared (Smith, 2007).

Unlikely Palaeozoic echinoids, which are rather similar in overall shape but show a remarkable variation in the plating structure of the test (e.g the number of columns of plates), post-Palaeozoic echinoids show a great variety of shapes with a fixed number of columns of plates in their test (Smith, 2005, 2007).

Regular echinoids test show pentaradial symmetry and consists of ten double columns of plates, five interambulacral zones and five ambulacral zones. Ambulacra and

interambulacra plates, whose number is variable in different taxa, bear tubercles on which the spines are attached (Fig. 46).

Peristome and periproct are the two major openings that characterized the test. The peristome, which has a circular shape, is located in the centre of the lower surface (oral surface). At the apex of the test lies the apical disc. This ring of ten plates encircles the anal opening and is always positioned on the aboral surface. The apical disc is composed of five genital and five ocular plates which surround a flexible plated membrane, named periproct, that contains the anus. Inside the test is a complex apparatus termed the Aristotle's lantern which comprises some 50 skeletal elements.

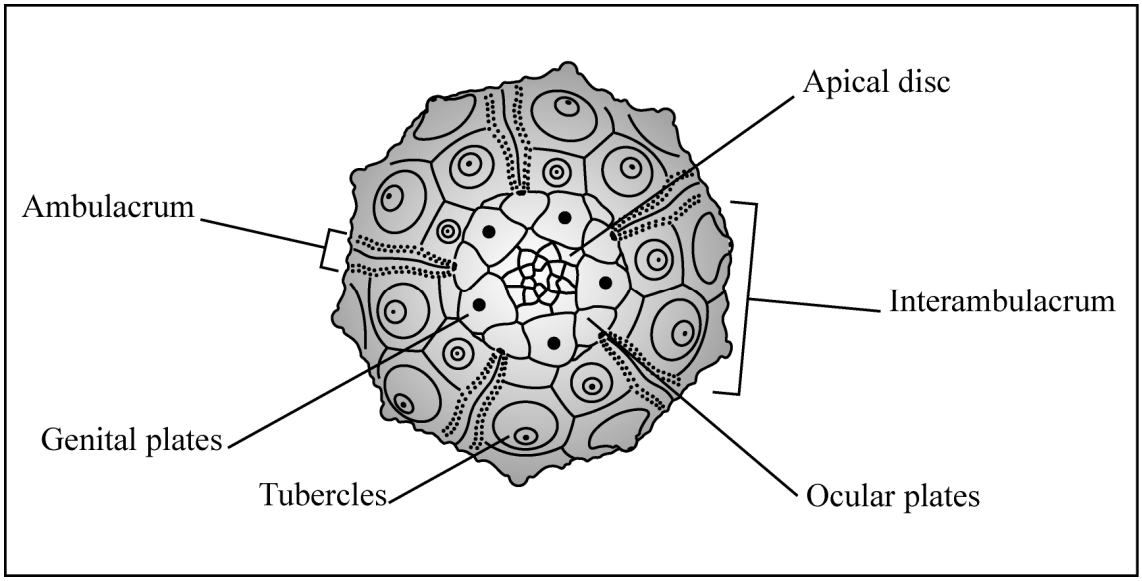

Figure 46. Main morphological features of the regular echinoid (cidaroid) test.

5.1.2. Regular echinoid mass accumulations in the fossil record

The fossil record of regular echinoids is poor if compared to that of irregular sea urchins. There are rare reports for accumulations of complete regular echinoids. Aggregation of thousands of exceptionally well preserved *Archaeocidaris*, which is considered a precursor (sister taxa) form to all modern echinoids (Smith 1984), occurs in the Pennsylvanian Whinchell Formation from Texas, (Schneider, 2001, 2003). Cidaroids also can form dense accumulation of complete specimens as documented by *Temnocidaris danica*, from Denmark (Gravesen, 2001). Other examples of high dense assemblages of regular echinoids were provide by Kier (1972) who described an accumulation of well preserved *Psammechinus philanthropus* within the Upper Miocene Yorktown Formation from Virginia and by Von Gert Bloos (1973) who reported an accumulation of *Diademopsis helvetica* from the Lower Jurasssic of the inner part of the South German Basin near Tübingen. More recently Jagt and Deckers (2010) described a dense fossil assemblage of the phymosomatid *Gautheria* from the Meerssen Member of the Maastricht Formation, which preserved lanterns, peristomial, apical disc plating and the spine canopy. A remarkable monospecific accumulation of regular echinoid spines, which are more resilient skeletal component than fragile regular echinoid test, were documented by Moffat and Bottjer (1999) in the Lower Triassic Virgin Limestone of Nevada. The paucity of regular echinoid in the fossil record contrasts with extant echinoid faunas, in which regular species are predominant (Kier 1977; Greenstein 1993). Kier (1977) attributed the paucity of fossil species of regular echinoids to their low preservation potential, which is related both to the skeletal construction and, largely, to their epifaunal lifestyle. Kier's hypothesis is discussed by Smith (1984) who stated that the poor fossil record of the regular echinoids is related to the fact that they evolved and diversified as grazers on firm or rocky substrata in shallow water environments, which are areas of active erosion where the preservation

potential is low. Through taphonomic actualistic experiments, Greenstein (1991, 1993, 1995) tested and modified Kier's hypothesis, considering that the skeletal architecture plays a more important role than life habits in the preservation potential of regular echinoids and that the discrepancy between fossil and extant abundance and diversity of regular echinoids may be an artefact of taxonomic methodology. In fact the classification of regular echinoids at higher taxonomic levels is frequently based on intact corona material, including lantern, tooth structures etc. (Smith 1990); this is in contrast with the regular echinoid fossil material that usually occurred as fragmented remains and therefore prevents the identification at the generic or specific level. The Miocene echinoid fauna of Sardinia reveals the same general pattern with 32 recorded genera (Comaschi Caria, 1972), of which 10 are regular forms (31, 25%) (Fig. 47A, B), such as *Schizechinus* and *Tylocidaris* (Fig. 48A, B). This value, which fits into the percentage (33%) of Miocene regular echinoid genera (Kier, 1977), is in contrast with those (52,6%) of the extant Mediterranean (Tortonese, 1979) (Fig. 47C, D).

Two Miocene mass accumulations of regular echinoids from Sardinia are analyzed. The first assemblage consists of a dense accumulation of a new taxon of phymosomatid echinoids, *Anisophyma carlinoi*, from the Lower Miocene Marmilla Formation of Central-Western Sardinia; the second regular echinoid accumulation comes from the Middle Miocene Gesturi Marls of Southern Sardinia. An integrated palaeoecological, taphonomical and sedimentological approach, provide a unique insight to understand the depositional histories and palaeoecology of these uncommon echinoid beds.

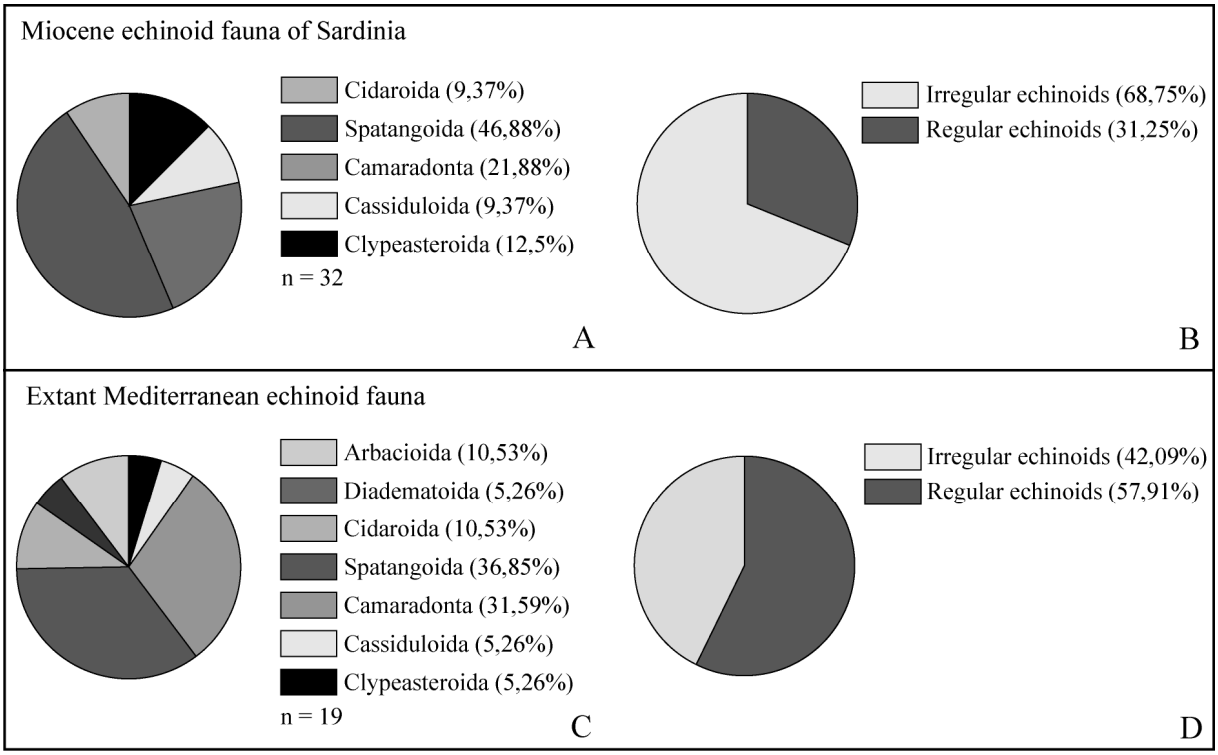

Figure 47. A) Relative abundance of Miocene echinoid fauna of Sardinia at generic level. B) Regular vs. irregular Miocene echinoid abundance at generic level. C) Relative abundance of extant Mediterranean echinoid fauna at generic level; D) Regular vs irregular extant Mediterranean echinoid abundance of at generic level. Data based on Comaschi Caria (1972) and Tortonese (1979); n = indicates the number of genera.

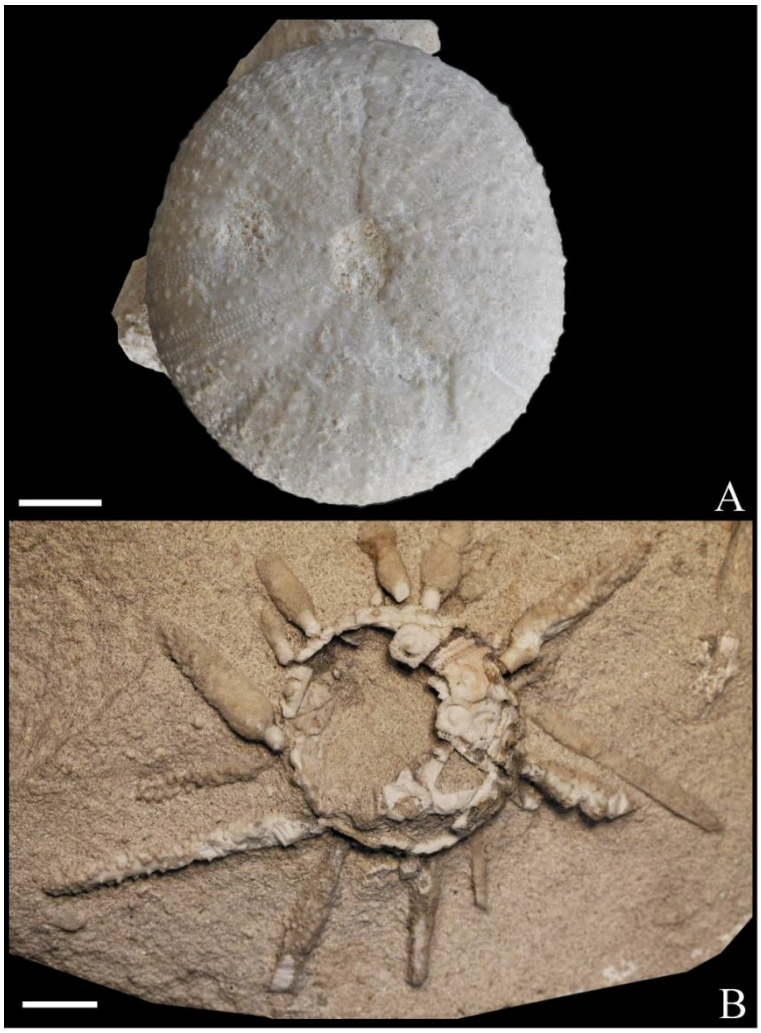

Figure 48. Two regular echinoid genus of the Miocene of Sardinia. A) *Schizechinus duciei* (Wright, 1855) from the Middle Miocene of Santa Caterina di Pittinuri; B) *Tylocidaris (Sardocidaris) piae* Lambert, 1907, from the Lower Miocene of Funtanazza.

5.1.3. Geological framework

The first regular echinoid assemblages are found in the Marmilla region (Fig. 4B), in Central Sardinia, within the Late Aquitanian to Early Burdigalian Marmilla Formation which belongs to the first sedimentary cycle of the Sardinian Basin. A second regular echinoid assemblage is located in the Campidano region (Fig 4C), in southern Sardinia, within the late Burdigalian to middle Langhian Gesturi Marls and belongs to the second sedimentary cycle.

5.1.3.1. Gennas (Villanovaforru, central Sardinia)

The phymosomatid echinoid assemblage originates from the locality Gennas (N39°37’19’’ – E8°52’34’’), 1 km south of Villanovaforru, a small village in the Marmilla region, Western-Central Sardinia (Fig. 49A, B). In this area a prevalently clastic sedimentary sequence belonging to the Oligo-Miocene crops out. This sequence starts with the Oligocene to Aquitanian Ussana Formation (Pecorini and Pomesano Cherchi, 1969) which consists of polygenic conglomerates, breccias, sandstone and siltstone. The facies of this formation range from continental to transitional and littoral environments (Pecorini and Pomesano Cherchi, 1969; Cherchi et al., 2008). The Ussana Formation is covered by a mainly fine-grained sediment succession, which has been reported in the literature to Ales Marls and Marmilla Formation (Cherchi, 1974; 1985; Assorgia et al. 1997). The Ales Marls Formation (Cherchi, 1974; 1985) consists of grey marls with sporadic thin turbiditic sandstones interbedded, which are considered to be bathyal deposits; the upper part of these deposits is ascribed to the Aquitanian based on their microfossil contents (Cherchi et al., 2008). The Ales Marls Formation is covered by the Marmilla Formation (Cherchi, 1985), in which the regular echinoid assemblage was found. This formation is a volcano-sedimentary sequence that consists prevalently

of fine sandstones, siltstones and marls with coarse sandstones, lavas and ignimbrites sporadically interbedded. The facies of the Marmilla Formation could be traced back from littoral to epibathyal environments. The Marmilla Formation is micropalaeontologically dated from the Late Aquitanian to Early Burdigalian (Cherchi, 1974; Cherchi, 1985; Pomesano Cherchi, 1971; Fornaciari and Rio, 1996).

5.1.3.2. Ussana (southern Sardinia)

The second regular echinoid accumulation is found within the Gesturi Marls (Cherchi, 1974), ca. 1.5 km south of the village of Ussana (N39°22’15’’ – E9°5’37’’), Southern Sardinia (Fig. 49A, C). In the Ussana area both the first and the second Oligo-Miocene sedimentary cycles crop out. This sequence starts with the Oligocene to Aquitanian Ussana Formation (Pecorini and Pomesano Cherchi, 1969) which consists of polygenic conglomerates, breccias, sandstone, siltstone and volcanoclastic sediments. The facies of this formation range from continental to transitional and littoral environments (Pecorini and Pomesano Cherchi, 1969; Cherchi et al., 2008). The Ussana Formation is covered by the siliciclastic facies of the Late Oligocene to Burdigalian Nurallao Formation. In this region the Nurallao Formation, which closes the first sedimentary cycle, consists exclusively of the Serralonga Sandstones Members, whose facies could be traced to littoral environments. The Nurallao Formation is unconformably followed by the Gesturi Marls (Cherchi, 1974), which belong to second Miocene sedimentary cycle. This informal unit, consist, in the lower-middle part of a monotonous hemipelagic fine-grained sequence of more than 500 m thick with sandy levels interbedded, whereas the upper part shows several tuffitic layers intebedded into the marl and arenitic facies. The Gesturi Marls, micropalaeontologycally dated to Middle Langhian (Cherchi 1974; Iaccarino et al., 1985), is locally heteropic with and followed by the Fangario Clay unit, which consist of bathyal clays and marls with high fossil content (Spano and Barca, 2002).

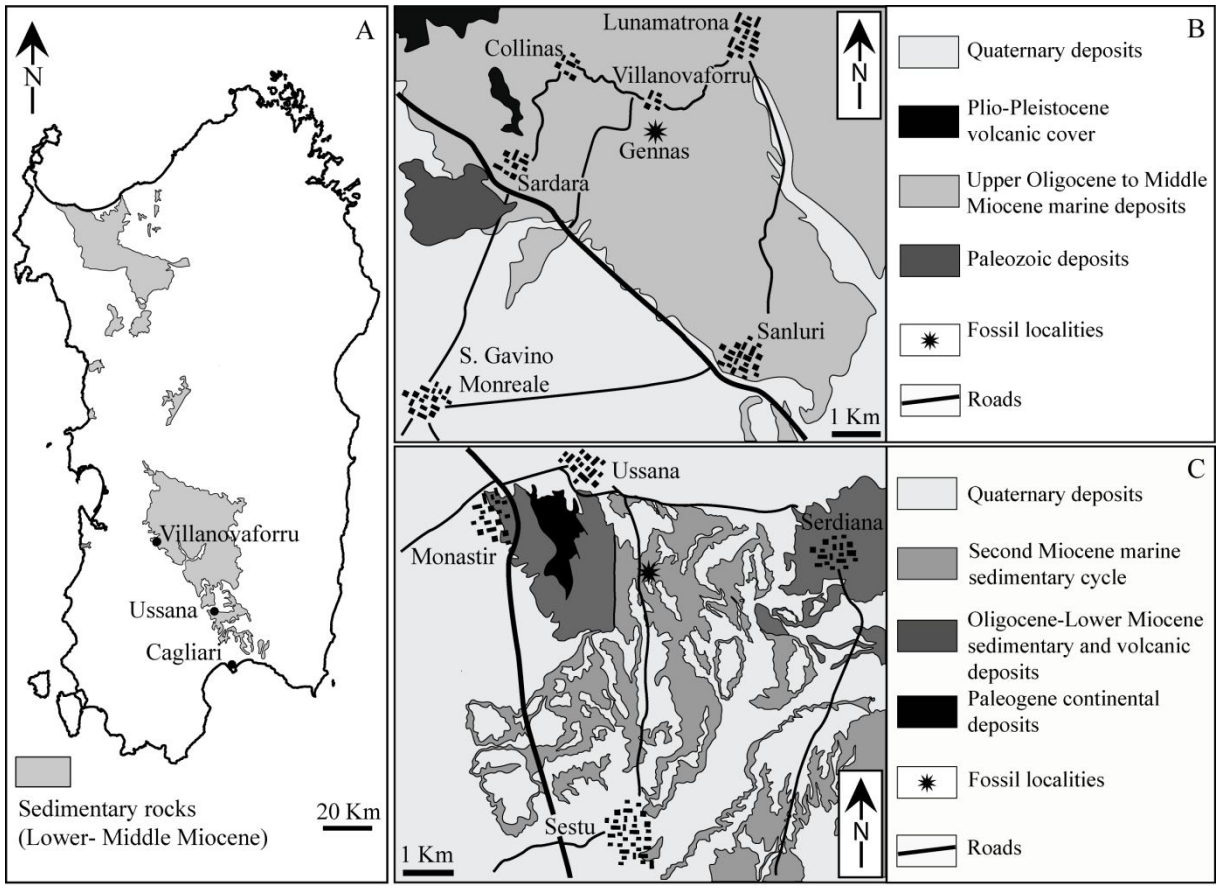

Figure 49. A) Distribution of Sardinia Miocene sedimentary rocks. B) Simplified geological map of the Villanovaforru area. C) Simplified geological map of the Ussana area. The asterisk indicates the site from which fossil echinoids have been collected.

5.1.4. Material and methods

A palaeontological, taphonomical, stratigraphical and sedimentological field and laboratory study, was made. Two thin (ca. 15 cm thick) stratigraphic interval of the Marmilla Formation and Gesturi Marls were investigated in detail. Faunal composition, diversity and abundance were described for each stratigraphic interval. The taphonomic signatures of individual specimens, such as preservation style, disarticulation, fragmentation, breakage, abrasion, encrustation etc., were observed. The fabric of the deposits, both in plan view and in cross section, and orientation of fossil material relative to the bedding were observed. More than one hundred samples are used for the taphonomic, sedimentologic and palaeoecologic studies. Actualistic experiments on regular echinoids based on published works (Allison, 1990; Kidwell and Baumiller 1990; Greenstein, 1991, 1993) are used for biostrationomic inference. The sedimentological study required analysis in thin section and observation of sedimentary structures in cut slabs; the mineral phases were evaluated using X-ray diffraction. For the X-ray diffraction analysis, samples were lightly ground in an agate mortar, and ~200 mg of the powder of each sample were packed into the sample holder. XRD analysis was performed using conventional θ-2θ equipment (Panalytical) with CuK_{α} wavelength radiation (λ = 1.54060 Å), operating at 40 kV and 40 mA, using the X'Celerator detector.

The phymosomatid specimens utilized in this study originate from the Marmilla Formation which crops out in the locality Bruncu de Gennas, 1km S of Villanovaforru, Central-Western Sardinia. Additional undetermined regular echinoid remains are found between Ussana and Sestu (Southern Sardinia), within the Gesturi Marls. All sedimentologic and palaeontologic samples are located at the Department of Earth Sciences of Cagliari University.

5.1.5. Stratigraphy and sedimentology

5.1.5.1. Villanovaforru-Sardara area

Recent, field-work in the Villanovaforru/Sardara region revealed a clastic sedimentary sequence ca 400 m-thick (Fig. 50). The sedimentary sequence can be subdivided into three units.

The lower part of this sequence mainly consists of sandy facies with conglomeratic intercalations. The observed sequence starts with a m-thick heterometric, polymictic conglomerate deposit (Fig. 51A) which consists of sub-rounded to rounded clasts with a range of diameter size from 2 to 10 cm. The clasts consist predominantly of metamorphic, granitic and quartz granules and pebbles. These conglomerates, predominantly supported by a sandy matrix, are crudely stratified and show evidence of imbrication. Within these coarse grained deposits very abundant disarticulated and randomly oriented ostreid fragments are found. The conglomerates are followed by ca 20 m-thick of well sorted, coarse to medium sandstones. Usually these sandstones show a massive aspect, although parallel and cross lamination and vertical burrows sporadically occur (Fig. 51B). Within the sandstones, decimetre-thick conglomerate intercalations, were frequently observed. These thin conglomerate levels are supported by a sandy matrix and show a high abundance of ostreid remains.

The middle part of the sequence is characterized by alternations of coarse to medium sandstones, and heterolithic fine grained levels (Fig. 51C, D, E). The sandstone deposits, which can reach plurimetric thickness (until 6 meters), appear massive and mainly consists of sub-angular to sub-rounded quartz grains. Within these sandy deposits large nodules can be frequently observed (Fig. 51F). Fine grained heterolithic levels consist of laterally persistent yellow to brown fine sandstones and mudstones

which are characterized by a wide range (spectrum) of sedimentary structures. Three main lithofacies are recorded: 1) yellow mudstones with undulated and planar parallel lamination; 2) yellow mudstones with apparent massive aspect; 3) interbedded hummocky cross stratified fine sandstone and mudstone. In the third facies gutter casts frequently occur. Hummocky cross stratification structures commonly show meter scale spacing and decimetre high (ca. 10-15 cm) (Fig. 51C, D). Gutter casts can reach up to 15 cm in width and 10 cm in depth (Fig. 51E). The bed contacts between the thick coarse sandstone deposits and fine grained levels are sharp. Complete and disarticulated fishes, belonging to families Clupeidae, Sternoptychidae, Scombridae and Gadidae (Sanciu, 2009, unpublished data), plant and algal remains are locally common within the fine grained levels.

The upper part of the sequence shows a greater homogeneity of lithology and sedimentary structures. This part of the succession, where the echinoid beds are found, consists of both massive and finely laminated siltstone and very fine sandstones; rarely mudstone and very fine siltstone show internal laminations. Massive medium to coarse grained sandstones, ca. one metre-thick, can be sporadically observed. The fossil content mainly consists of pectinids belonging to genus *Amussium*, regular echinoid spines and disarticulated fish remains. The detailed investigation of ca. 15 cm -thick interval (Fig. 52A) of the Marmilla Formation, which contains the regular echinoid beds, shows yellow silicified mudstone (siltstones to claystones) that exhibit a millimetre-scale lamination. Individual laminae range from 0.5 mm to 5 mm in thickness. Lamination is generally parallel and gentle undulating. This interval is apparently not affected by bioturbation. The contact between the laminated levels are sharp but there is no evidence of erosive contact.

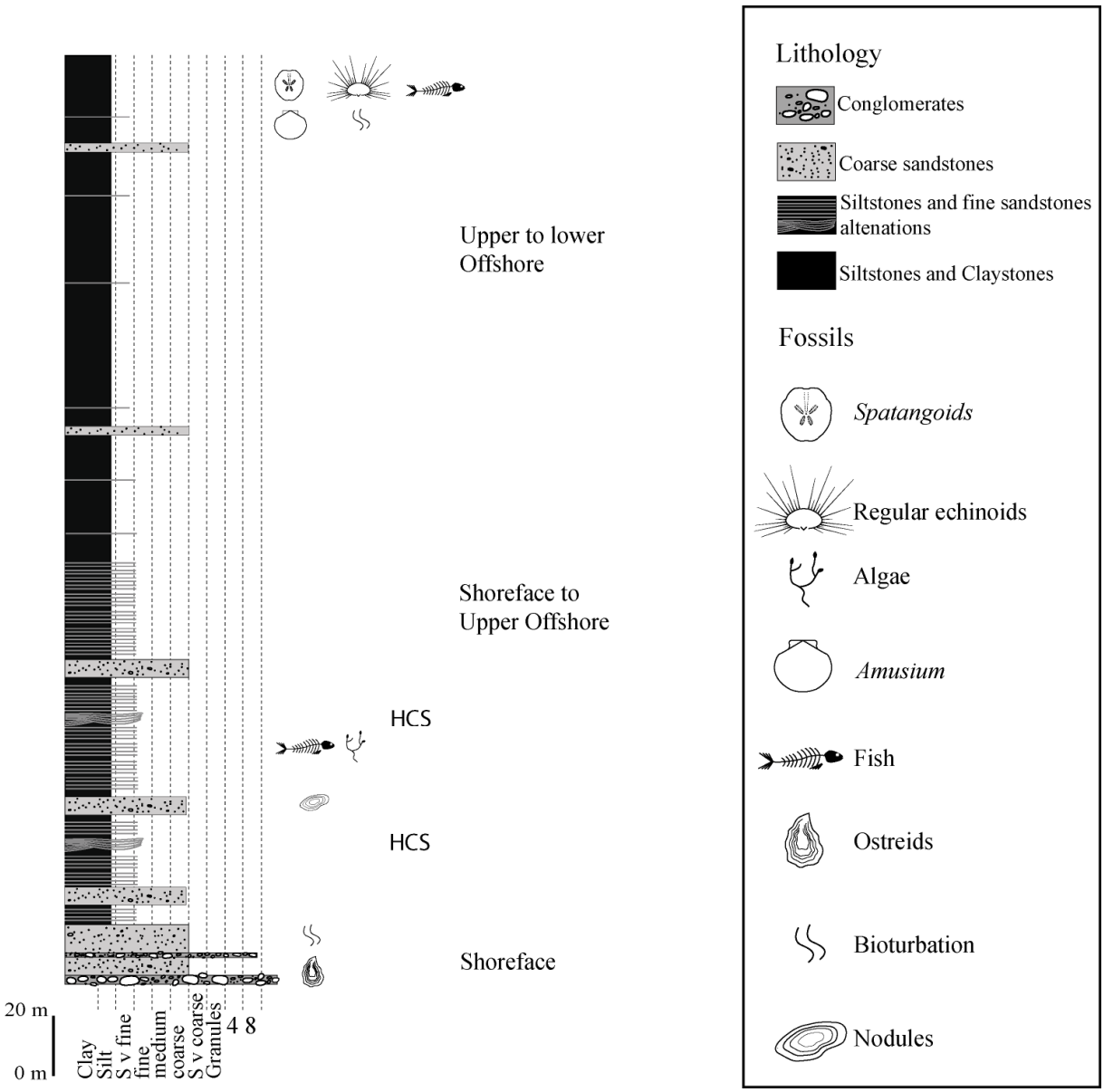

Figure 50. Interpretative stratigraphic section of Villanovaforru-Sardara area. This sedimentary succession can be subdivided into three main units: a lower unit, characterized by coarse grain sediments of the shoreface environment; a middle unit, showing alternations of coarse sandstone and fine grained sediments which depositional environments ranging from shoreface to upper offshore; an upper unit which mainly consists of massive and finely laminated siltstones and claystone deposited from upper to lower offshore.

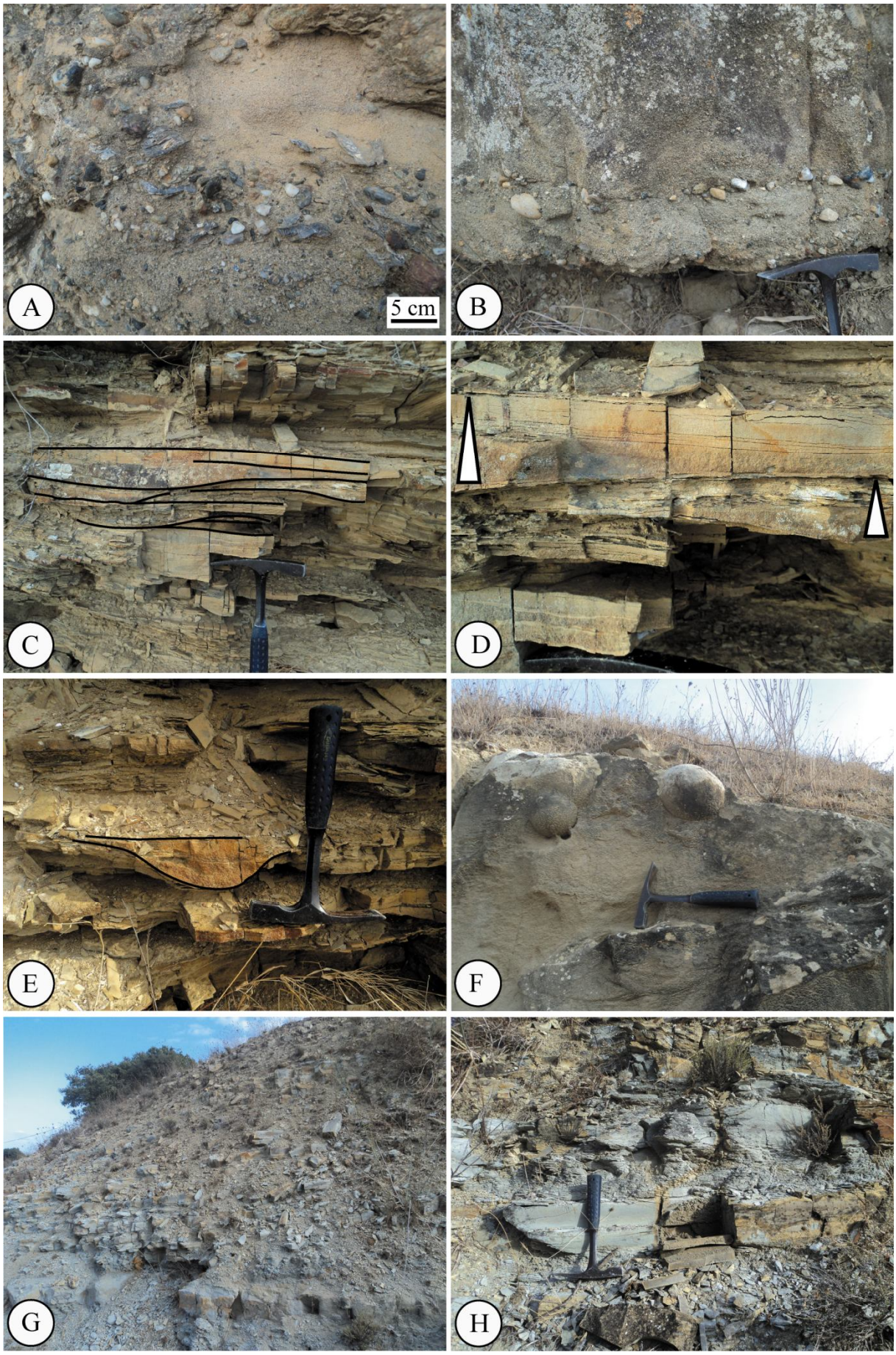
A
5 cm
B
C
D
E
F
G
H

Figure 51. Mainly facies recorded in the Sardara-Villanovaforru section: A, B) Coarse grained sandstones with conglomeratic intercalations and ostreid remains (Serra Truiscu locality) which characterized the lower part of the succession; C) Fine grained facies, sandstones and siltstones, with undulated, planar parallel lamination and HCS. D, E) Detail of fined grained facies showing HCS and gutter casts. F) Massive coarse sandstones. These meters-thick sandstone are found within a mainly fine grained sequence in the lower middle part of the section (Turriga locality). G, H) massive and finely laminated sitstone and claystone facies of the middle-upper part of the section.

5.1.5.2. Ussana area

The outcrop situation in the Ussana/Sestu area is relatively poor. The regular echinoid bed is found within an interval of the Gesturi Marls characterized by finely (millimetre-thick) laminated fine sandstones and siltstones. The studied interval of Gesturi Marls, ca. 15 cm-thick, (Fig. 52B) shows a fine grained sequence with a vertical grain-size change from fine sandstone to mudstone. The lower part of the samples shows sandstone/mudstone intercalations. The sandstone levels are irregular, sometimes discontinuous and range from 2 mm to 1 cm in thickness. Often the lower bed contacts are sharp and erosive. The middle part of the samples consists of 2.5 cm thick fine massive sandstones in which the fossil echinoid remains are concentrated. The clasts are composed mainly by quartz grains with mm-sized clay chips, which float within a fine matrix sandstones. The degree of quartz grains rounding varies from angular to sub-angular with grain sizes ranging from 0.1 to 0.2 mm. This fine sandstone appears graded, without evidence of lamination, preferred clast orientation or bioturbation. The lower bed contact is gentle erosive while the upper bed contacts is sharp. The upper portions of the samples show finely laminated alternation of fine sandstone and mudstone. Individual laminae are 1mm to 2 mm in thickness. Lamination is generally gentle undulatory and sometimes lenticular. The sandstone levels show slightly erosive bed contacts. In this upper part of the samples sporadic spines occur.

5.1.5.3. Depositional environments of Sardara/Villanovaforru sedimentary succession

A siliciclastic fining-upward (retrogradational) marine succession crop outs in the Villanovaforru/Sardara area. Three main units were distinguished. The lower unit consists of massive, coarse sandstone and interbedded polymictic conglomerates which could be trace to shallow water, shoreface environments. The middle unit consist of alternations of plurimetre-thick coarse, massive sandstone and fine grained, sandy and muddy, levels. The thick coarse massive sandstone levels could be trace to shoreface environment while the heterolithic fine grained levels, which show several sedimentary structures such as finely undulated and planar parallel laminated levels, hummocky cross stratification and gutter casts. These could be related to the alternation of quiet-water sediment fall-out and combined storm flows in the upper offshore. The most distinctive sedimentary structures are the hummocky cross stratification; although the genetic mechanism of the hummocky is debated (Dumas and Arnott, 2006), there is a general consensus that these sedimentary structures form during storms between fair-weather and storm wave base in open marine environments (Dott and Burgeois, 1982), particularly in the proximal and the middle part of the upper offshore. The sedimentologic features of the upper unit of the sequence, such as the prevalence of fine grained sediments and their massive and finely laminated aspect, document an increasing of depth and the evolution of the sedimentary sequence from upper to lower offshore.

5.1.5.4. Depositional environment of Gesturi Marls in the Ussana area

Lithological and sedimentological aspects, such as the alternation of millimetre-thick sandstone and siltstone levels, the presence of slightly erosive bed contacts, the undulatory and lenticular lamination, allow to refer this heterolithic facies to distal part of a storm dominated upper offshore.

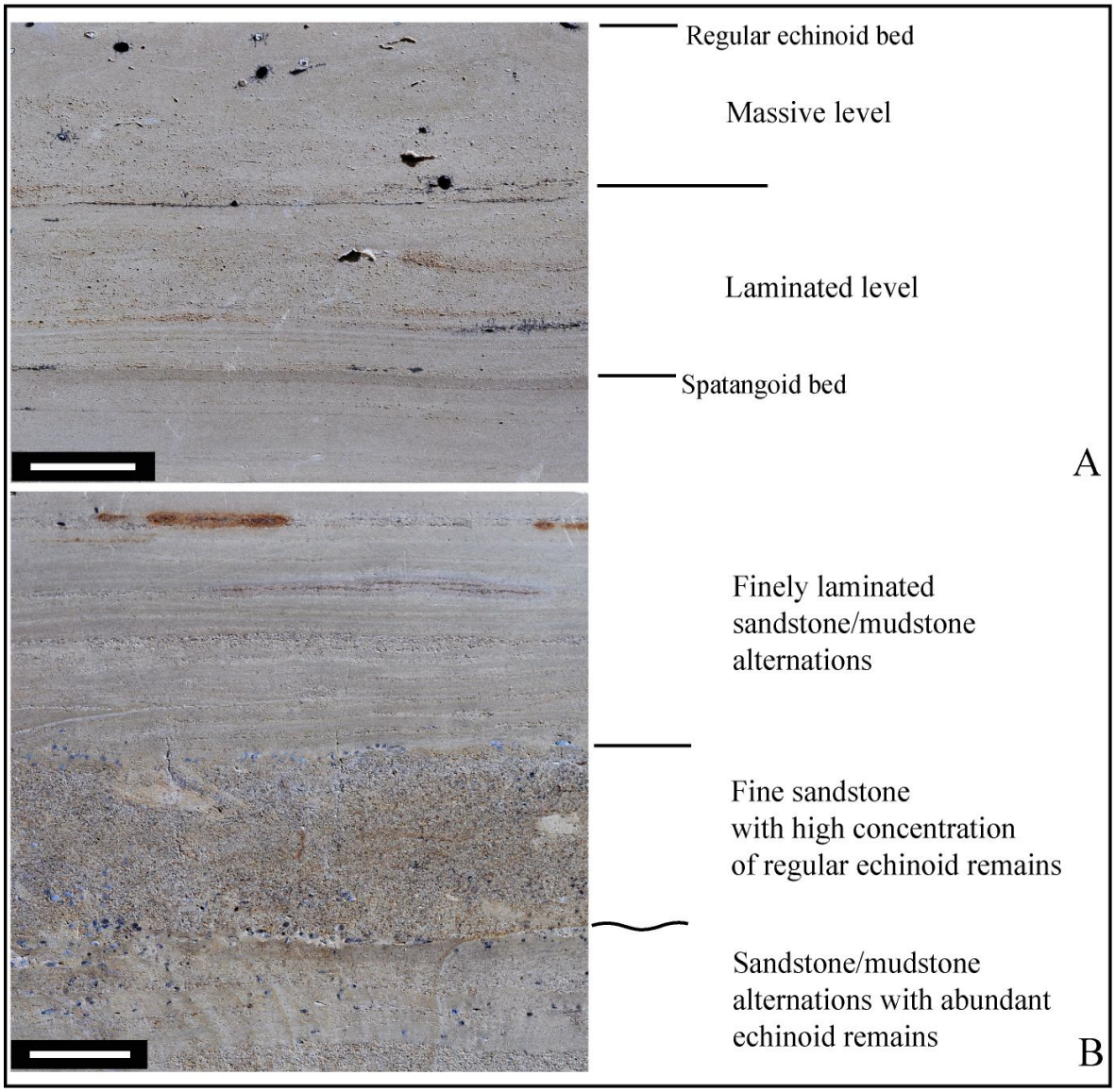

Figure 52. A) Polished slab from Marmilla Formation, Gennas (Villanovaforru); note the occurrence of two monospecific phymosomatid and spatangoid echinoid assemblages. B) Polished slab of Gesturi Marls, Ussana; the regular echinoid remains are concentrated in the lower part of the fine sandstone level. Scale bars = 1 cm.

5.1.6. Taphonomy

5.1.6.1. Phymosomatid echinoid assemblage from the Marmilla Formation

Preservation style – The palaeontological content mainly consists of a monospecific assemblage of the regular echinoid *Anisophyma*, a new genus of phymosomatids, the remains of which form a 2 centimetre-thick bed. The lower part of the fossiliferous bed consist exclusively of disarticulated spines and plates, scattered on the bedding planes. Complete tests are concentrated in a single bedding plane in the upper part of the bed (Fig. 52A and 53A). All echinoid tests are parallel to bedding and show a preferred dorsoventral orientation with 52% of tests in life position (Fig. 54B). These remains are typically preserved as external and internal moulds. Few specimens retain their skeleton, which is not preserved in original skeletal mineralogy; diffractometric analysis performed on test and spines remains indicates that they have partially been replaced by SiO_2 (Fig. 56). Sporadically small bivalves occur.

Disarticulation and fragmentation – The echinoid remains show different states of disarticulation (Figs. 53 and 54A), such as intact tests with articulated spines (Fig. 53 B,C), denuded coronas, disarticulated spines and rare isolated ambulacral and interambulacral plates. Unlike the sequence indicated by Greenstein (1991), the samples show an inverted condition: articulated tests with their spines lack the apical disc. On the oral face, the Aristotle's lantern can be observed. Thus, with exception of the spines and sporadically corona element (isolated ambulacral and interambulacral plates), there are no disarticulated skeletal elements such the apical and peristomal plates. Both tests and spine do not show evidence of damage or breakage.

Abrasion – The echinoid remains are not abraded; in the external moulds fine details such as the crenulation of the tubercles and the longitudinal striation of the spine, can be observed.

Size and orientation of spines – Complete spines show a wide length size range. They range from 5 mm to more than 60 mm in length. The disarticulated spines are randomly orientated in plane view (Figs. 53A and 58A, B). In cross section the spines are from concordant to slightly oblique to the bedding plane.

Density and test size frequency distribution – The test remains are found in high density, with maximum abundance of six individuals per dm^2. The test size frequency distribution, measured on 50 specimens, is dominated by a single mode between 16 and 28 mm test diameter (Fig. 55).

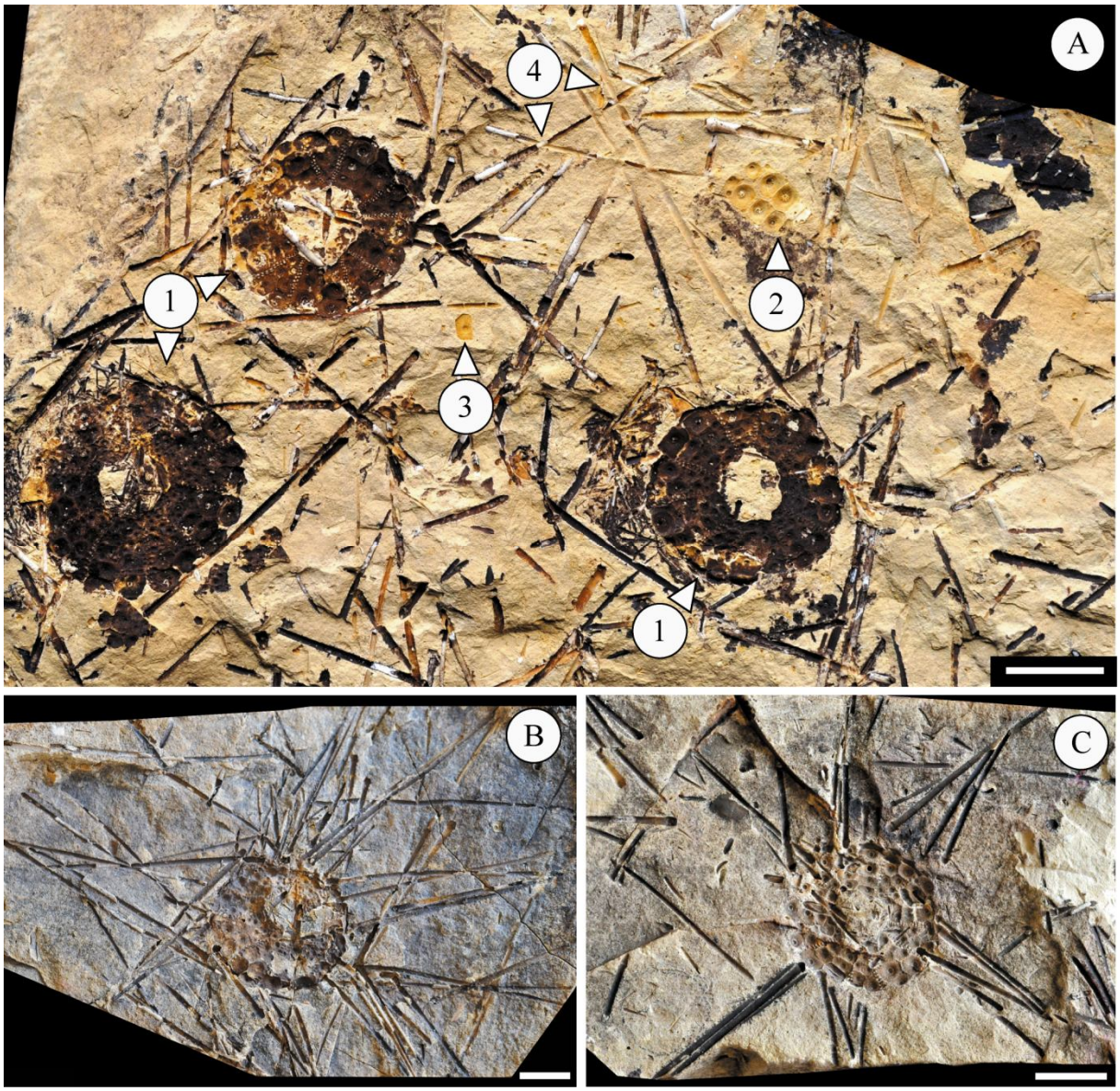

Figure 53. Preservation state of the *Anisophyma* assemblage of the Marmilla Formation, Villanovaforru. A) 1) Complete tests without spine attached (denuded tests) (NHMW2013/0026/0001); 2) Partially articulated interambulacral plates; 3) Single interambulacral plate. 4) Intact spines. B and C) Complete test with their spine canopy (MDLCA23521). Scale bars = 1cm.

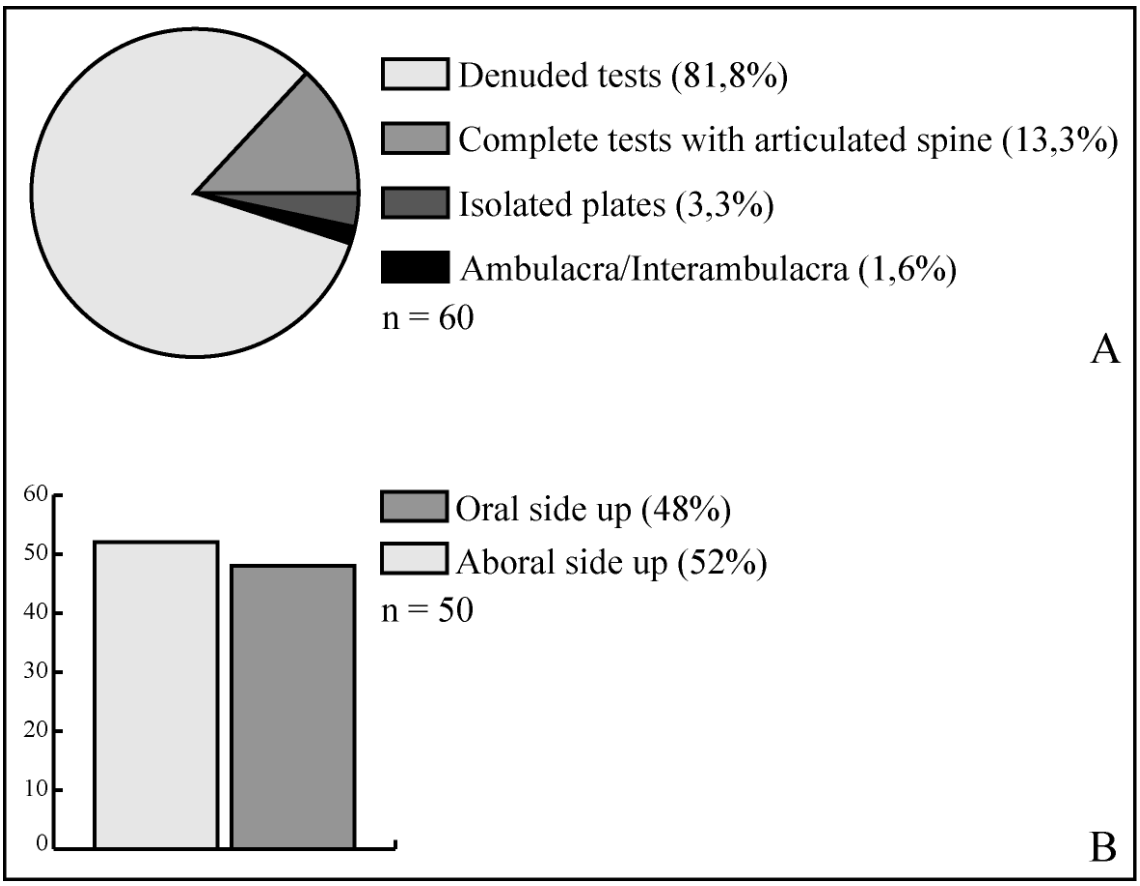

Figure 54. A) Data summarizing the states of articulation of the phymosomatid remains of the Marmilla Formation. The echinoid remains mainly consist of complete and denuded test, while isolated plates and ambulacra or interambulacra sporadically occur. B) Dorso-ventral orientation of complete and denuded echinoid tests.

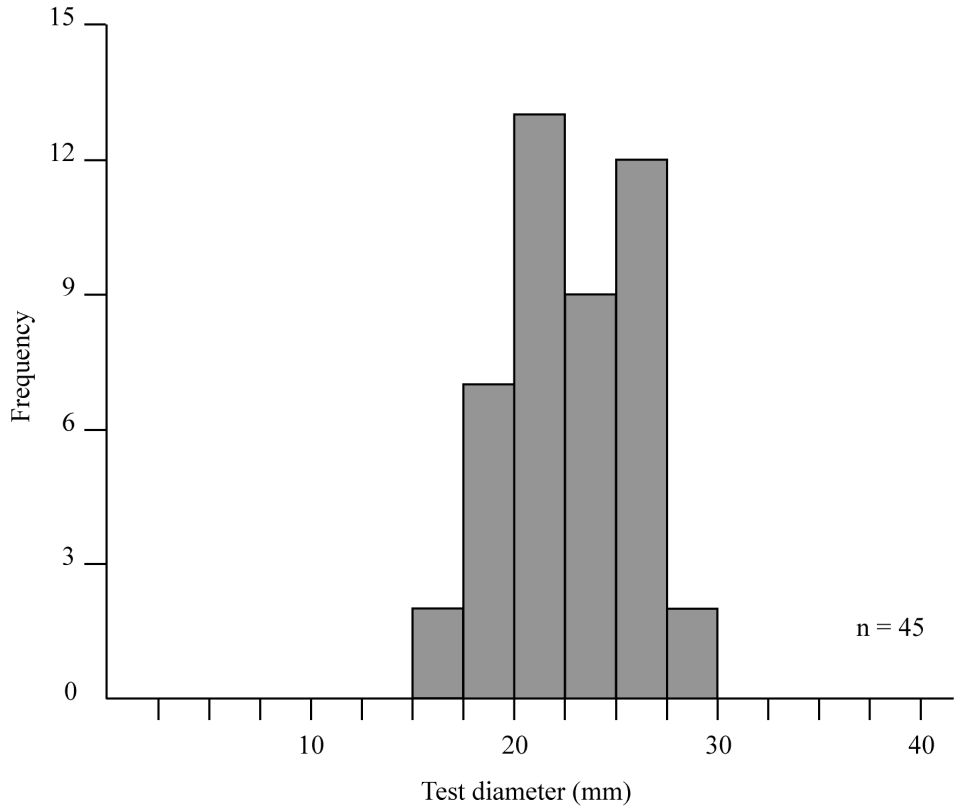

Fig. 55. Size frequency distribution of *Anisophyma carlinoi*; n indicates the number of specimens.

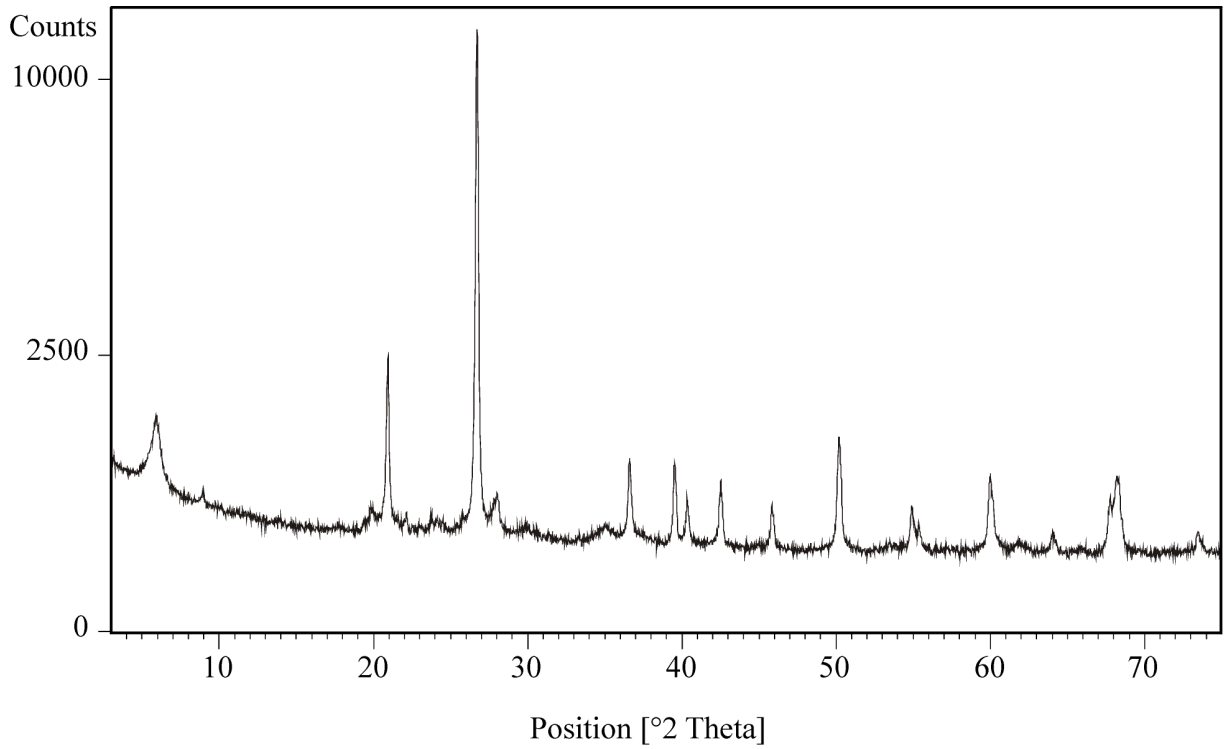

Figure 56. X ray diffratometric analysis of phymosomatid test remains; the analysis shows that the original skeletal material are replaced by quartz.

5.1.6.2. Regular echinoid accumulation from the Gesturi Marls

Preservation style – The palaeontological content mainly consists of a monospecific spine accumulation bed belonging to an undesribed regular echinoid (Fig. 57A, B). Fossil abundance varies vertically within the sequence analyzed. The echinoid remains are abundant in the laminated levels of lower part of the sequence, below the slightly erosive contact; these remains occur within both sandstone and mudstone laminae. The echinoid remains reach a very high density in the ca 2.5 cm-thick sandstone level of the middle part of the sequence (Fig. 52B), above the erosive contact and are concentrated in the lower part of this sandstone level. The fossil remains tend to be very uncommon in the upper sandy/muddy laminated levels. All the remains are concordant to subconcordant to the bedding plane.

Disarticulation and fragmentation – The high fossiliferous sandstone level is mainly characterized by complete and fragmentary spines and coronal plates; rarely fully articulated tests with their spine canopy and complete tests without spines attached (denuded corona) occur (Fig. 57B).

Abrasion – Various degrees of abrasion occur; relatively pristine plates with tubercle crenulation and spines with longitudinal striation are mixed with considerably (heavely) abraded plates and spine with no visible fine details.

Orientation of spines – The spines range from 5 mm to 65 mm in length and are largely intact. In plan view, the disarticulated spines are consistently bi-orientated (Fig. 58C, D). In cross section, the spines are from concordant to slightly oblique to the bedding plane.

Density – The echinoid remains, which mainly consist of spines and plates, are found in high density. Usually, the remains are in contact and the echinoid deposit range from matrix to shell-supported (from densely packed to loosely packed deposit, sensu Kidwell and Holland, 1991).

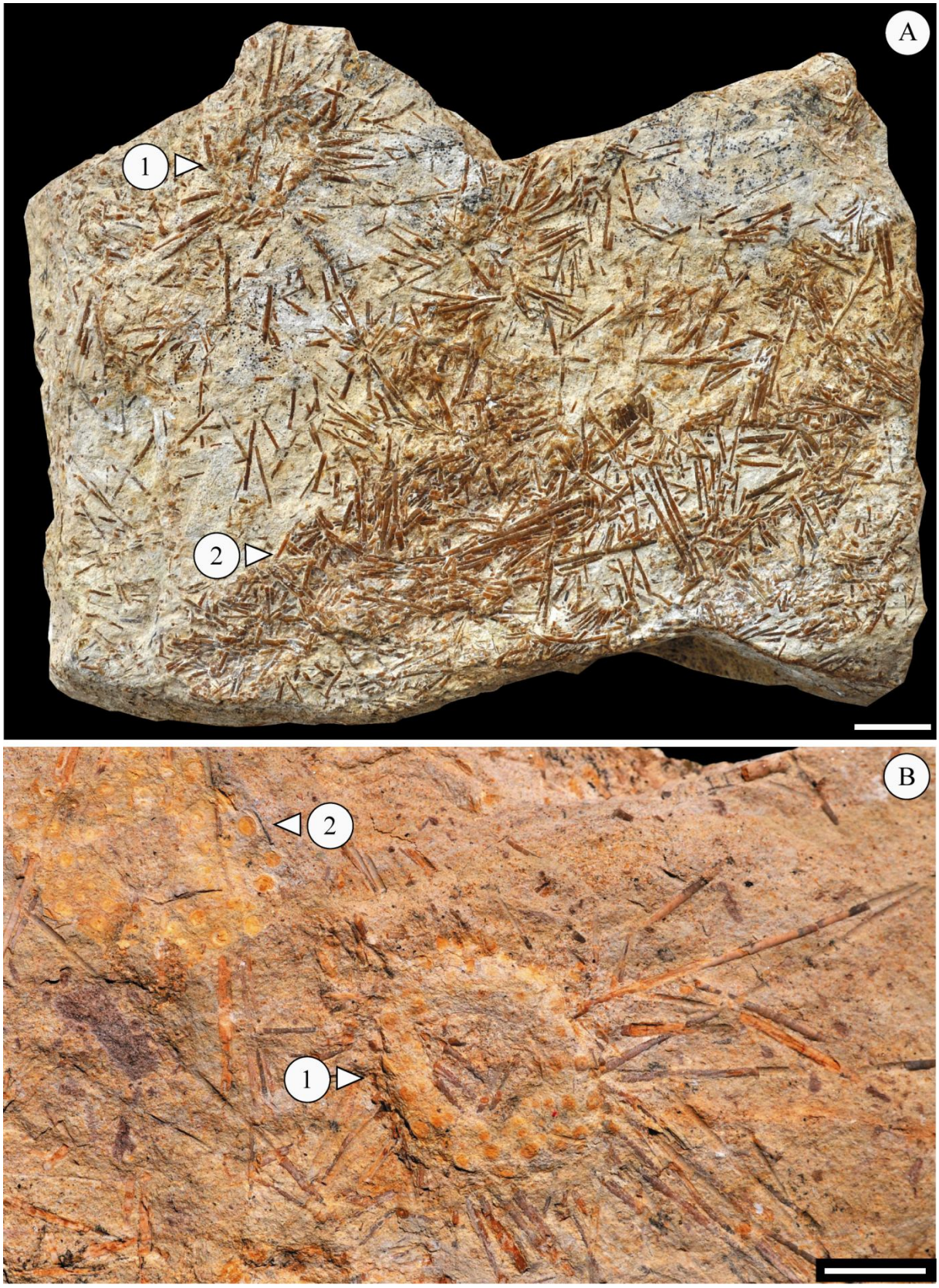

Figure 57. State of disarticulation of regular echinoid remains of Gesturi Marls, Ussana: A) 1) Incomplete test with spine attached; 2) Intact and broked spines (MDLCA23519). B) 1) Complete test with their spines attached and 2) denuded test (MDLCA23520). Scale bars = 1cm.

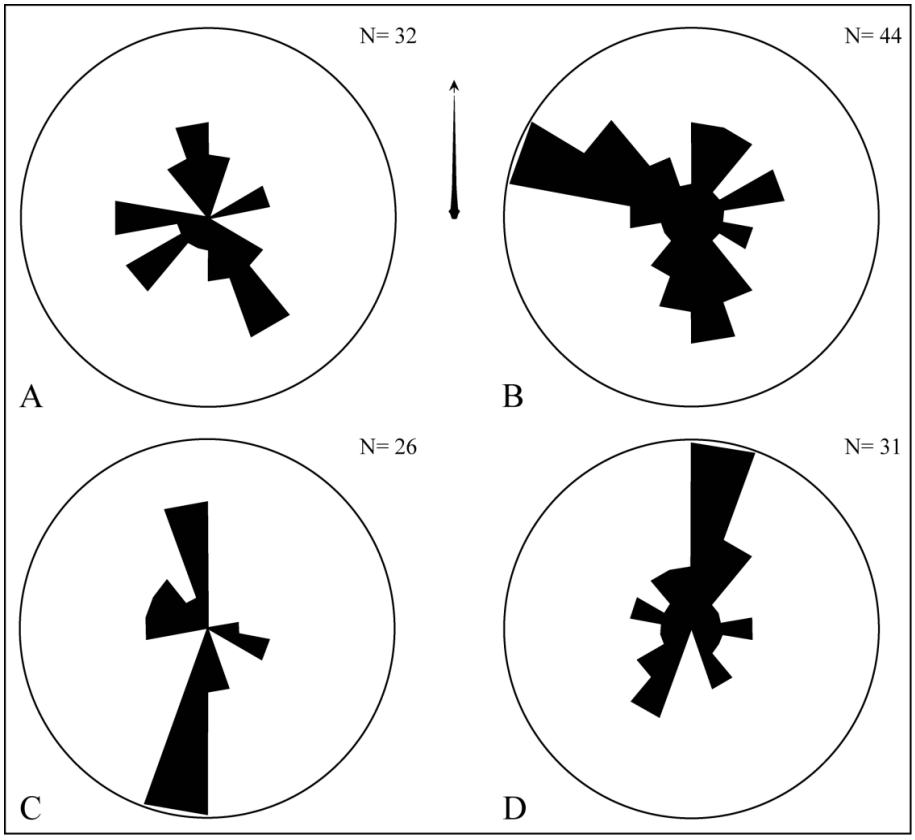

Figure 58. Rose diagram indicating the orientation in plan view of the complete spines: A and B) Regular echinoid assemblage from Marmilla Formation, Villanovaforru; C and D) regular echinoid assemblages from Gesturi Marls, Ussana. n indicates the number of spine counted.

5.1.7. Discussion

Taphonomic features of fossil regular echinoids, such as preservation styles, degree of articulation, orientation of spines, preferred plan and cross orientation etc., can be used to reconstruct physical (e.g. transport and wave reworked) chemical and biological (e.g. predation, bioturbation) processes, which characterized the depositional environment. Therefore, the biostratinomical studies of echinoids permits carrying out palaeoenvironmental and palaeoecological interpretation at a high level of confidence (Nebelsick, 1995, 2004).

5.1.7.1. Disarticulation and fragmentation

Actualistic studies based on experimental and field observation contribute to clarify the taphonomic processes which affected the echinoid tests and to infer palaeoenvironmental parameters. Field and laboratory experiments conducted on regular echinoids (Allison, 1990; Kidwell and Baumiller, 1990; Greenstein, 1991) show that their preservation is related to intrinsic features, such as constructional morphology and mode of life, and extrinsic factors such as temperature, oxygen content and bioturbaton. Taphonomic experimental investigation conducted by Kidwell and Baumiller (1990) and Greenstein (1991), respectively on two species of *Strongylocentrotus* and other four Caribbean species of regular echinoid belonging to genera *Diadema, Eucidaris, Echinometra* and *Tripneustes,* reveal that reworking can induce rapid disarticulation of spines and precludes the preservation of fragile complete tests. Different echinoids show a similar sequence of skeletal disarticulation, with semi quantitative states of decay ranging from intact (State 1) to completely disarticulated corona (State 6). There are, however, differences in time of disarticulation for each regular echinoid. In these experiments, *Diadema antillarum* disarticulated in few days in decay conditions and in few hours in tumbling conditions (Greenstein, 1991),

showing the low preservation potential of Diadematidae in comparison to other echinoids. Donovan and Gordon (1993) through a semiquantitive analysis of the fossil record of the same four taxa, demonstrate a good agreement with the taphonomic experiments.

Regular echinoids can frequently suffer lethal and non-lethal damage and breakage which could be mainly related to impact. Direct observation of impacts on echinoids are rare; Ebert (1968) suggests that echinoid damage caused by impact from rolling cobbles and against rocks is a common feature in the shallow water high energy environments where the echinoids can be dislodged, particularly during storms. Experiments conducted by Strathman (1981) on different regular echinoids, such as *Diadema, Echinometra, Eucidaris* and *Lythechinus* denote that 1) under impact against a hard substratum the spines absorb the impact energy and can prevent test damage, 2) the strength of test varies among species and 3) within the species, strength under impact can increase with size. In addition, spine connections to the tests were more resistant to impact than spine fragmentation or test destruction.

These taphonomic experiments can be used, for interpreting the echinoid fossil record and can shed light on the origin of regular echinoid accumulation beds. The disarticulation states of the phymosomatid remains allow to distinguish two taphofacies. The first taphofacies (tf 1) exclusively consists of disarticulated remains while the second taphofacies (tf 2) is mainly characterized by complete and denuded tests. The preservation states of phymosomatid remains in the tf 2 lead to exclude a strong transport or reworking and allow the autochthony of the assemblage to be inferred.

As for the regular echinoid bed of the Gesturi Marls, the occurrence of the remains in various states of disarticulation, such as complete and denuded tests, isolated plates and pristine and broken spines, implies moderate transport and reworking.

5.1.7.2. Encrustation and bioerosion

Encrustation and bioerosion frequently occur in intertidal and shallow sublittoral environments; their occurrence increase with productivity and decrease with higher sedimentation (Leschinsky et al., 2002) and could therefore provide palaeoecological and taphonomical information. The robust and well shaped irregular echinoid, such as *Echinolampas* and *Clypeaster* (Nebelsick et al., 1997; Santos and Mayoral, 2008; Belaustegui et al., in press) are frequently affected by sclerobiont signatures. Regular echinoid tests can also offer hard substrate for encrusting and bioeroding organisms. Epibiont colonization was reported in fossils as well as in extant species of regular echinoids.

Schneider (2003) described the oldest known syn-vivo brachiopods and bryozoan epibionts on the long spines of *Archaeocidaris* from Pennsylvanian (Texas) while serpulid polychaetes and barnacles are the most frequent epibionts on the spines of the living species *Stylocidaris affinis* (Tortonese, 1979).

Wilson (2012) documents encrustation on cidaroids in the Matmor Formation (Callovian) of southern Israel by serpulid, bryozoans, brachiopods etc.

Kidwell and Baumiller (1990) reported the presence of encrusting and boring organisms, such as bryozoans, barnacles and serpulids on *Phymosoma* of the Upper Cretaceous British Chalk while Greenstein (1995) documents gastropods bioerosion and encrustation by calcareous green algae on extant regular echinoid *Tripneustes ventricosus*. Both the studied regular echinoid assemblage do not show evidence of syn-vivo epibionts or post mortem encrustation and bioerosion; this taphonomic aspect can be related to low productivity and brief possibility for colonization after death.

5.1.7.3. Palaeoecology of regular echinoids

Regular echinoids are epifaunal invertebrates which, as evidenced by Smith (1984), since the Jurassic have evolved and diversified as grazer, feeding on algae or seagrass. Most regular echinoids inhabit shallow water, high energy, environments on rocky bottom or stable substrate and they can attached themselves in holes, crevices or under stone, as documented for example for the long spine sea urchins *Diadema antillarum* and purple sea urchin *Strongylocentrotus purpuratus* (Randall et al., 1964; Scheibling and Stephenson, 1984). However, regular echinoids, can also occur on soft sediment from sublittoral to bathyal zone where they usually ingest sediment and small invertebrates. The species *Centrostephanus longispinus* and *Stylocidaris affinis*, for example, are adapted to inhabit sublittoral sandy and muddy areas of the Mediterranean Sea (Tortonese, 1979; Mortensen, 1928, 1940). Although the two regular echinoid mass occurrences in Sardinia differ markedly in origin, the taphonomic and sedimentologic evidence indicates that both echinoid assemblages, could represents communities which inhabited soft-bottom environment, below the normal (fair weather) wave base.

5.1.7.4. Gregarious behaviour and mass mortalities

Although the taphonomic and sedimentologic signatures of the two fossil regular echinoid beds differ, they are characterized by high density of remains. While the high density of regular echinoid spines found within the Gesturi Marls is due (is the result) to physical aggregation, the remarkable high density of the phymosomatid assemblage could be related to ecological factors. Mass accumulations are reported for extant regular echinoids such as *Diadema*, *Centrostephanus*, *Strongylocentrotus* and *Lytechinus* (Andrew and Underwood, 1993; Miller et al., 2007; Andrew and Byrne, 2007; Peterson et al., 2002). Randall et al. (1964), Bauer (1976), Sammarco (1980) and Miller et al. (2007) document high density association of *Diadema antillarum*, that usually range from 0.02 to 0.05 individuals/m^2 (Forcucci, 1994; Miller et al., 2007). *Centrostephanus rodgersii*, whose usual density ranges between 0.5 to 6 individuals/m^2 (Andrew and Underwood 1989), sometimes forms dense aggregation with more than 60 individuals per square meter (Andrew and Byrne, 2007). Moore et al. (1963), Camp et al. (1973) and Peterson et al. (2002) reported aggregations of *Lytechinus variegatus*, with density ranging from 43 to up to 600 individuals per square meter.

High densities of extant regular echinoids are mainly related to protection to predation and spawning. Miller et al. (2007), documented a positive association of adult and juvenile abundance of the long spine sea urchin *Diadema antillarum* and retain that the high density of adults of this long spine urchin could provided protection from predators through a tangle of spine. This can reduce predation rates of conspecific juveniles. A similar behaviour has been observed in *Strongylocentrotus* by Tegner and Levin (1983) who suggested that the structure of high density populations of *Strongylocentrotus franciscanus*, which usually show bimodal size-frequency distribution, could be indicative of size - selective predation on these urchins. The bimodality size distribution

is therefore a consequence of an increase in vulnerability of sea urchins to predation related to increase of adult-size and the microhabitats change from cryptic to open habit. Alternatively, the high density aggregation of regular echinoids could be related to spawning activity. High density aggregations of *Diadema antillarum* and *Strongylocentrotus* have even been observed during spawning season and could be related to increase (to maximize) of successful fertilization (Bauer, 1976; Pennington, 1985). Research conducted by Levitan (1989) and Lessios (1995) on *Diadema antillarum* suggests that the population density is an important factor in fertilization success. Levitan (1989) also denote an inverse relationship between body size and density of urchins, and retain that small-size and high density is a strategy to maintain fecundity and survivorship in periods of reduction of food availability.

5.1.7.5. Origin of phymosomatid echinoid assemblage

On the basis of the taphonomic features, the phymosomatids mass occurrence represents a rapidly buried autochthonous accumulation (Fig. 59). The preservation of complete test, 13.3% of which retain their spine canopy, and the preferred orientation of the specimens, parallel to bedding and in life position suggests minimal reworking (minimal disturbance by currents) and short residence time of dead echinoids on the sea bottom. The lacks of the apical disc in the specimens that retain the spines is, apparently, in contrast to the decay sequence indicated by Greenstein (1991). However, as evidenced by Smith (2007) and Jagt et al. (2010), the preservation of apical disc in the phymosomatids is particularly rare, because the apical plates are only loosely connected to the corona and thus usually missing in the fossil specimens. The wide size range of the complete spines, from 5 mm to 6 cm, and their random orientation in plan view lead to exclude long transport.

Smothering of the echinoids (obrution) is a common cause of death for echinoids because their water-vascular system is susceptible to clogging by fine sediments (Rosenkranz, 1971; Schäfer, 1972). Obrution is very rapid burial (from few hours to few days) of intact organisms and, as evidenced by Seilacher at al. (1985), is one of the main genetic mechanisms to preserve completely articulated multi-element skeletons, such as echinoderms, and to generate fossil Lagerstätten. An obrution events permanently buries the organisms through a suddenly large influx of sediment, which can prevent the decay on the seafloor or, in the case of mobile benthos, to extricate themselves (Brett et al., 1997; Dornbos and Bottjer, 2001). An obrution deposit usually shows two main peculiar aspect: 1) the present of intact, dead or alive, organisms and the 2) burial layer (Brett, 1990; Brett et al., 1997). Commonly the burial layers consist of barren structureless mudstone or siltstone (Brett, 1990; Brett et al., 1997). The typical geological agents that

cause the obrution events includes turbiditic currents, ash falls and storms (Brett, 1990; Dornbos and Bottjer, 2001). During storms e.g., the amount of sediments in suspension can be large (Reineck and Singh, 1972); the fraction of fine grained sediments could be transported to the deep shelf setting and deposited in low water energy environment. Sudden influx of this suspended high dense fine grained material could have smothered and buried a living or freshly dead echinoid population. The obrution hypothesis is consistent with sedimentological observations. The phymosomatid mass accumulation forms a single bed within a fine grained succession (from fine siltstones to claystones), which show parallel, undulated lamination presumably related to storm deposition in the lower offshore.

The occurrence of well-preserved regular echinoid assemblages can also be related to the low temperature of deep water environments. Kidwell and Baumiller (1990) and Banno (2008) through laboratory experiments on the regular echinoid *Strongylocentrotus* tested the role of temperature and oxygen content in organic decomposition. The authors conclude that low water temperatures inhibit the decay more than anoxia, which play a major role in excluding potential bioturbators and scavengers. Laboratory experiments conducted by Banno (2008) on the spatangoid *Schizaster* confirm these observations. Therefore these experiment may lead to reconsider the origin of echinoderm Lagerstätten not only as the product of obrution and/or stagnation events.

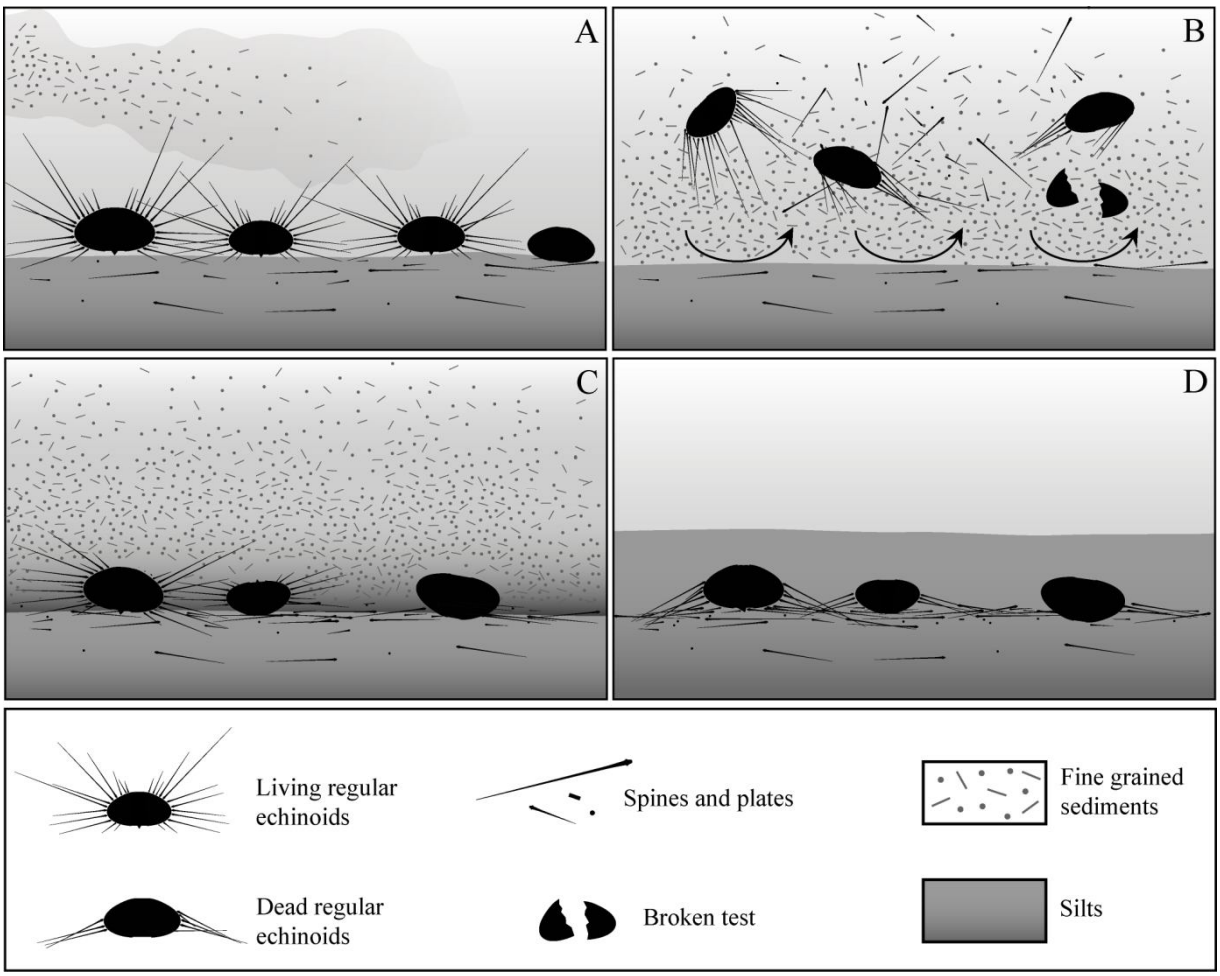

Figure 59. Biostratinomic pathways followed by the phymosomatid echinoid assemblage: A) Rapid influx of fine grained sediments by storm; B) Reworking of echinoids; C) Partial decay with disarticulation of spines and apical disc; D) Definitive

5.1.7.6. Origin of regular echinoid concentration bed from the Gesturi Marls

The taphonomic features of the regular echinoid beds within the Gesturi Marls, such as the high concentrated echinoid remains, mainly consisting of disarticulated pristine and broken spines and isolated coronal plates, with very rare complete tests retaining their spine canopy, suggest high energy depositional conditions and permit to consider this monospecific regular echinoid bed as a parautochthonous/allochthonous deposit including both significantly reworked material and fresher material. Shell transport and reworking could be also corroborated by the preferred bi-direction orientation of spines in plan view.

Sedimentary analyses support this hypothesis. The studied 15 cm thick interval shows an alternation of sandstones and mudstones levels presumably related to storm deposition. Vertical size changes and variation in sedimentary structures, from massive fine sandstone to finely laminated sandstone/mudstone alternations, indicate changes in energy environment and in rates of sedimentation. The regular echinoid accumulation bed has a gentle erosive lower bed contact with minimal scouring that, presumably, marks an episode of erosion of sediment under current activity. The fossiliferous level is graded, with the echinoid remains concentrated in the lower part.

These taphonomical and sedimentological inferences lead to interpret the high dense regular echinoid accumulation as a single or composite tempestite deposited in the distal part of the upper offshore. Sediment deposition during storms commonly produces distinctive sequence of facies (Aigner, 1985). As denoted by several authors Kreisa, (1981), Kumar and Sanders (1976) and (Hayes, 1976), storms frequently generate shell pavement and hardpart concentration through scouring, winnowing, suspension and transport.

As suggested by Kreisa (1981), storm generated sedimentary features such as layer thickness, sedimentary structures and preservation style of fauna, could be related to the depth of water in which the facies formed. The sedimentologic and taphonomic features such as a gentle erosional base, a graded shell layer with, reworked, parautochthonous fauna, followed by parallel lamination allow to interpret the deposit as a distal tempestites as described by Aigner (1985).

5.2. Spatangoids

5.2.1. General overview on the morphology and ecology of spatangoids

The echinoid belonging to the order Spatangoida, commonly know as heart urchins, were found in all the sea and oceans of the world, and vary in their geographical distribution from highly localized to highly cosmopolitan. Spatangoids are a group of irregular echinoid predominantly adapted to an infaunal mode of life, and they are able to live in virtually all types of marine sediment (Ghiold, 1988; Ghiold and Hoffman, 1989). However, some spatangoids have adopted an epifaunal life style, particularly those species living in the deep sea. Recorded depths of spatangoids range from sublittoral to abyssal depths (> 6000 m) (Mortensen, 1950, 1951), and therefore they are one of a small number of echinoid groups to have successfully colonized the deepest of marine waters.

Spatangoids have an extensive fossil record dating back to the Early Cretaceous (Villier et al., 2004). Currently the earliest spatangoid is *Toxaster africanus* from the Valanginian. During this period the appearance of morphological innovations, such as ambulacra arrangement (organization), development of fascioles, diversification of the function of spines, evolution of special tube feet for gas exchange, are mainly related to the adoption an infaunal lifestyle (Fig. 60A, B). These morphological innovations allowed the spatangoids to diversify quickly and to become the most diverse echinoid clade, consisting of 25% of the extant echinoid species (Villier and Navarro, 2004; David et al., 2009).

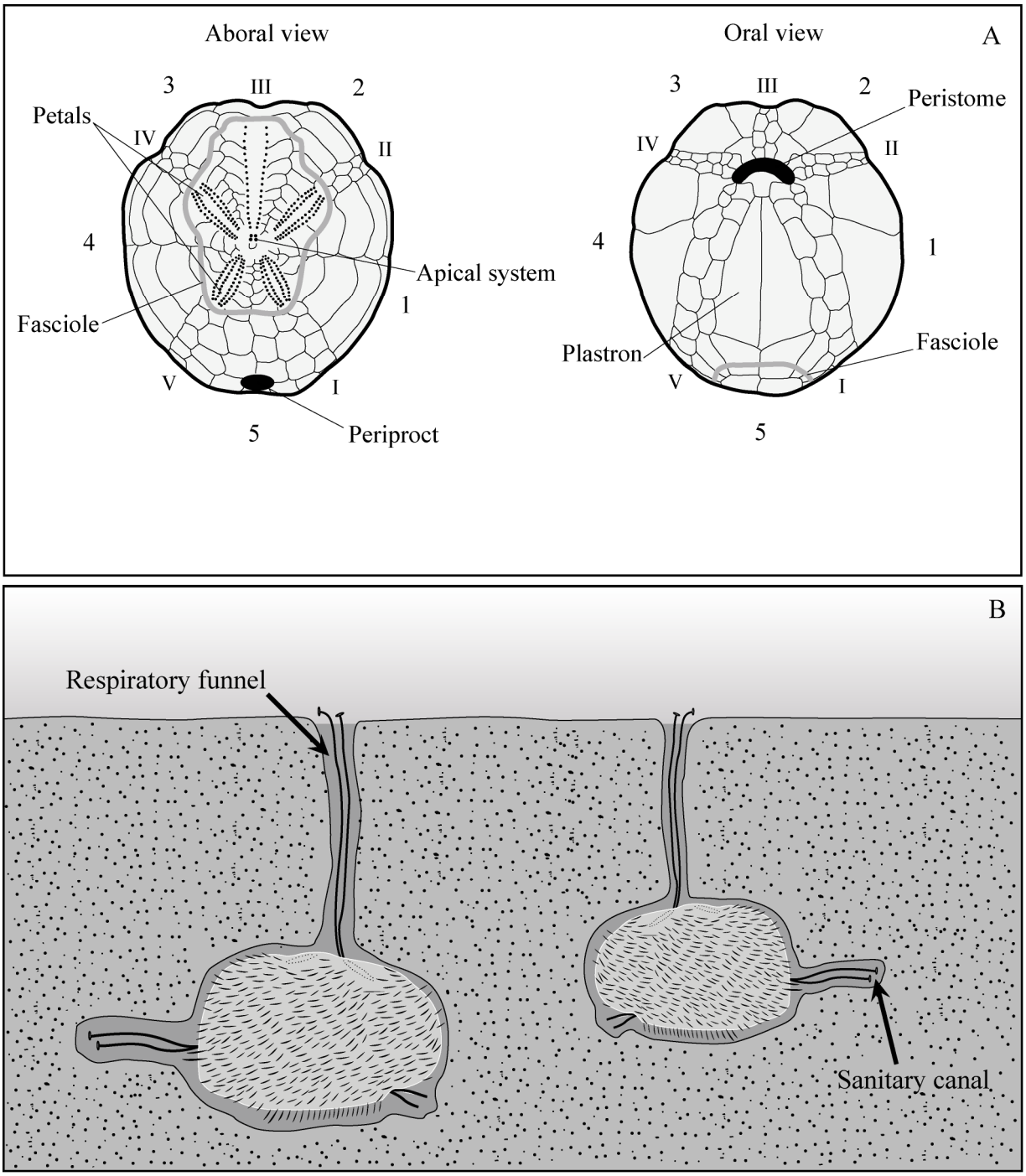

Figure 60. A) Main features of external morphology of the spatangoid *Brissopsis lyrifera*; Roman numbers indicate the ambulacra columns while Arab numbers indicate the interambulacral columns. B) Infaunal lifestyle of *Brissopsis lyrifera* within muddy sediments. This echinoid burrows through the sediments about 20 mm to 10 cm below the water/sediments interface; a respiratory funnel connects the urchins to the surface (Hollertz and Duchêne, 2001).

5.2.2. Mass accumulation of spatangoids

Although the spatangoids are widespread in the fossil record, they were rarely described to occur in mass accumulations.

Mass accumulation of very well-preserved spatangoid *Echinocardium orthonotum* occurs in the Pliocene Yorktown Formation of Virginia (Kier, 1972). The preservation of these echinoids in a chaotic style lead Kier (1972) to infer that they had not been preserved in life position but, instead, were caught up in storms currents, and subsequently buried by sediment soon after death in a nearshore environment.

A similar origin was proposed by Radwański and Wysocka (2001) for the mass accumulation of *Echinocardium leopolitanum* from the Middle Miocene of Ukraine. In this case the echinoids, which are preserved in a haphazard manner, often preserve their complete spine canopy and are apparently unaffected by taphonomic filtering, such as disarticulation, fragmentation, encrustation, etc.; these biostratinomic observations lead the authors to infer the origin of this echinoid accumulation by rapid and definitive burial related to storms.

Other examples of spatangoid dense accumulation is described by Néraudeau and Breton (1993), that reported an assemblage of very well preserved *Macraster cf. polygonus* from the Albian sediments of Normandy.

Here a monospecific mass accumulation of *Brissopsis* from the Marmilla Formation is decribed. This spatangoid mass occurrence was found four centimetres below the phymosomatid mass accumulation described above.

5.2.3. Taphonomy

Preservation style – The palaeontological content consists of a monospecific *Brissopsis* assemblage, which remains occupie a single bed (Fig. 52A and Fig. 61A). All the spatangoid tests are crushed and preserved as external or internal mould. The specimens mainly are found in life position (60%) (Fig. 62B).

Disarticulation – Different state of disarticulation were observed (Figs. 61A, B, C and 62A). The remains consist of intact test with their spine canopy, denuded tests, large test fragments, small test fragments, petaloid fragments, isolated plastron and disarticulated spines. Fragments of spines, such as portions of the shaft, were rarely observed. Usually the spines appear complete and retain their proximal portion.

Abrasion – The test remains do not show evidence of abrasion. In the external moulds of both complete test and large and small fragments fine details, such as the crenulation of the perforate tubercles, can be constantly observed. The surfaces of the spines are finely longitudinal striated.

Encrustation – Observations of the external mould of the complete tests and large fragments do not show evidence of encrustation, bioerosion or predation.

Size and orientation of spines – Complete spines show a length range from 1 mm to 1.2 cm. The disarticulated spines are randomly oriented in plan view (Fig. 62C).

Density and test size frequency distribution – The complete test and fragments are found in high density. A maximum abundance of seven complete individuals per square decimetre occur. The tests, which are crushed, show a length range from 1 cm to 7 cm.

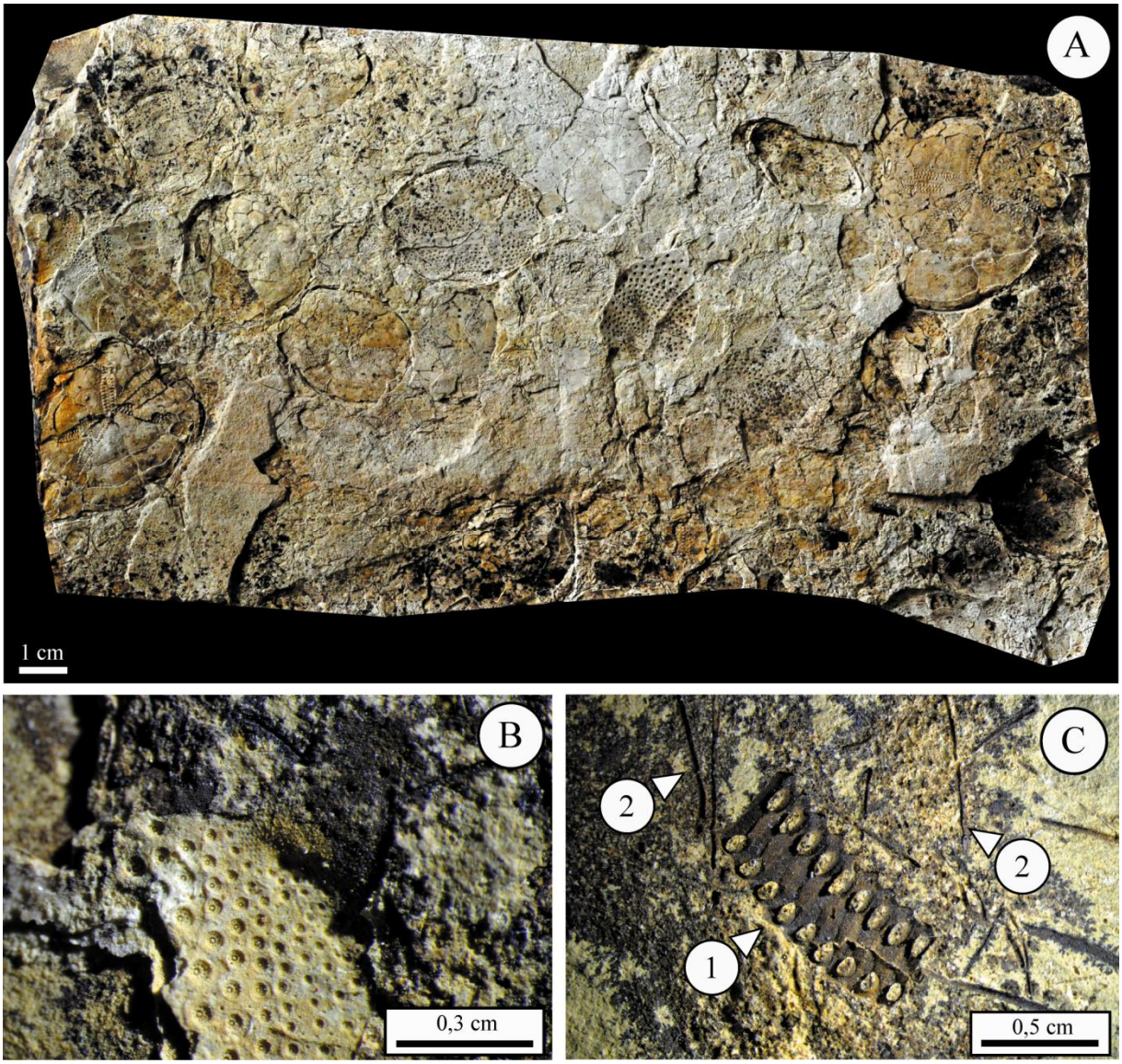

Figure 61. A) *Brissopsis* mass accumulation layer, which found 4 cm below the Phymosomatid layer. This accumulation consist of both fragmented and complete *Brissopsis* specimens with the minute spines scattered on the bed (MDLCA23523); B) Fragments of *Brissopsis* test showing fine details such as the crenulation of perforate tubercles; C) 1) Portion of the petaloid and 2) spines of *Brissopsis*.

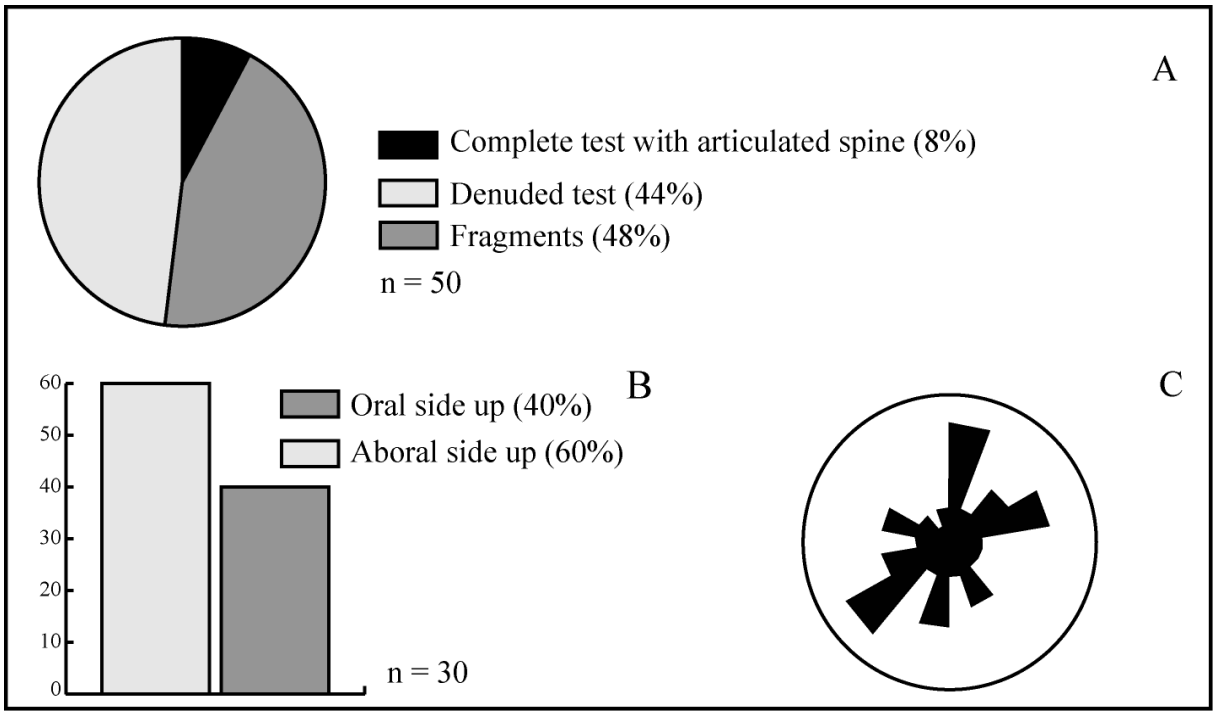

Figure 62. Taphonomic data of *Brissopsis* assemblages. A) Pie diagram showing the disarticulation states of spatangoid tests. B) Dorsoventral orientation of tests, with prevalence of echinoid in aboral side up. C) Rose diagram showing random orientation of spines in plan view.

5.2.4. Discussion

5.2.4.1. Ecology of the *Brissopsis*

The irregular echinoid *Brissopsis* is an infaunal deposit feeders spatangoid which inhabits soft bottom, muddy areas, burrowing to a depth from 2 to 10 cm (Hollertz and Duchêne, 2001), although epibenthic behaviour occasionally occur (Fig. 60B).

This taxon, which is characteristic of the temperate region and which occurs in the Mediterranean and in the Atlantic and Indo-Pacific oceans (Mortensen, 1951), is one of the deepest-water recent spatangoids living in outer shelf environments, from the circalittoral to bathyal (Mortensen, 1951; Néraudeau et al., 2001; Hollertz, 2002). The extant species *Brissopsis lyrifera* e.g., is known to occur in the present Mediterranean region frequently between 60 and 200 m depth but become very abundant in the deeper bathyal zone (Prouho, 1988; Tortonese, 1979; Néraudeau et al., 2001) where dense monospecific populations were observed (Féral et al., 1990). Typical densities vary between 5 to 60 individual per m^2 (Tunberg, 1991; Ursin, 1960). Similar observations were made by Hollertz et al. (1998), which reported a high dense association of *Brissopsis lyrifera* and the ophiuroid *Amphiura chiajei* at depths from 50 to 200 m in the North Sea.

5.2.4.2. Exhumation and emergence at the sediment surface

Taphonomic signatures of the *Brissopsis* accumulation, such as the presence of intact tests with their spine canopy, denuded tests, both in life position and reworked, and fragments, allow inferring that the *Brissopsis* specimens could have suffered exhumation on the bottom sea. However it is difficult to prove if exhumation happened before or after the echinoids died.

Exhumation and emergence at the sediment/water interface could be related to three main factors:

1) Storm induced current
2) Intense endobenthic bioturbation activity
3) Hypoxic sediment conditions

In order to clarify the origin of the spatangoid assemblage these three aspect were considered and discussed:

1) The corona of *Brissopsis* is delicate and fragile (Mortensen, 1951). The high percentage of intact tests and the presence of their complete minute spines both articulated and scattered on the bed allow to exclude severe and (sustained) long post mortem transportation.
2) The finely laminated muddy levels within the *Brissopsis* layer occur not seem affected by bioturbation. Therefore exhumation and breakage by bioturbation can be excluded.
3) As evidenced by Smith (1984), when infaunal irregular echinoids undergo an environmental stress they are able to come up to the sediment surface, where they commonly die. Hypoxic conditions can induce infaunal species to leave their positions in the sediment and lie exposed on the bottom. Stachowitsch (1984)

reported a mass mortality of macroepifauna and macroinfauna in the Gulf of Trieste, presumably caused by oxygen deficiency. This phenomenon involved even a population of the burrowing echinoid *Schizaster canaliferus*. The echinoids progressively spotted alive on the sediments surface (emerge from the sediment from their burrows) and after a week all echinoids were dead and had lost most of their spines. Even *Brissopsis lyrifera* is reported as a species sensitive to hypoxia (Diaz and Rosenberg, 1995; Rosenberg et al., 1997). Similar mass migration of benthic infauna (including *Brissopsis lyrifera*) to the sediment surface was recorded in the North Sea with low values of oxygen (ca 2 ml/l) (Dyer et al., 1983).

5.2.4.3. Disarticulation

Few experimental studies of spatangoid decay have been conducted under both natural and laboratory conditions. Nebelsick et al. (1997) reported the biostratinomic history of the spatangoid *Schizaster canaliferous* during a mass mortality events under oxygen deficiency conditions in the sublittoral, low energy, environment of northern Adriatic. This infaunal echinoid emerged from the sediments and rapidly died. Spine are lost within four days after death while the naked tests remain whole for long time (months) and retain the same orientation with the aboral side facing upwards. Laboratory studies were conducted by Banno et al. (2008) on *Schizaster lacunosus* from Japan in order to verify the decay processes at different water temperatures. The results documents that decay rates are strongly controlled bay water temperature: in high and medium temperatures (30°C and 20°C) the spines disarticulated within 5 days respectively and 4 weeks while lower water temperature drastically inhibit the disarticulation processes with the spines that remain attached to the test for more than 10 months.

The *Brissopsis* remains from Sardinia show different states of disarticulation from intact test with their spine canopy to small test fragments and disarticulated spines. This taphonomic gradient from well preserved specimens to highly fragmented material could indicate a high concentrated time-averaged deposit or mixed dead and living specimens which were mobilized and transported by currents (e.g. storms).

5.2.4.4. Encrustation and bioerosion

Although the spatangoids are prevalently infaunal echinoids, epibiont signatures, such as bioerosion and encrustation, can affect their tests. This phenomenon is recorded in the extant spatangoids as well as in the fossil forms. Nebelsick et al. (1997) studied the biostratinomic pathways of a population of *Schizaster canaliferus*, during an anoxia-related mass mortality event in the Northern Adriatic Sea (Gulf of Trieste). In this sublittoral, low energy, environment the spatangoid tests remain intact for a long time and encrusting organisms, such as serpulids, ascidians, barnacles etc. colonized the test between 11 and 20 months after death.

Sclerobiont signatures, including bioerosion and encrustation, were described by Zamora et al. (2008) on the typical Cretaceous spatangoid *Micraster* from Olazaguita Formation (Northern Spain). Encrustation and bioerosion on spatangoids were also documented respectively by Giusberti at al. (2005), who described a specimen encrusted by a verrucid barnacles, in their study on the spatangoid *Ovulaster protodecimae*, from the Danian Scaglia Rossa Formation, and by Beu et al. (1972) on *Pericosmus* and *Lovenia* from the Miocene of New Zeland.

High dense mass accumulation of *Brissopsis* forms a shellground ('echinoid carpet') which can offer a hard substratum for secondary tierers in a soft bottom environment.

Although the *Brissopsis* assemblage consist both articulated and fragmented specimens, that could indicate long residence time of the echinoid tests on the bottom sea after the definitive burial, thus a potential long opening for colonization window, the tests do not show evidence of encrustation or bioerosion. Therefore this aspect could be related to low productivity and unfavourable ecological conditions in deep shelf environments.

5.2.4.5. Origin of the spatangoid mass accumulation

Taphonomic signatures of the *Brissopsis* assemblage, which occur in a single bedding plane, such as complete tests with their spine canopy, denuded test, large and small fragments and disarticulated spines indicate multiple cohorts of mixed long and recently dead echinoid remains. In order to explain the origin of this echinoid mass occurrence two different mechanisms, such as mechanical aggregation by current and shell accumulation under low sedimentation rate have been considered:

It is plausible that the spatangoid mass accumulation can be the result of exhumation and transport by currents (e.g. by storms). Both the taphonomic signatures, such as the high percentage of fragments and of complete specimens oral side up oriented (40%), and sedimentologic features corroborate this hypothesis. However, it is unlikely that mechanical aggregation currents would create an allochthonous monospecific accumulation with a high percentage of complete, fragile infaunal spatangoid tests, particularly in distal shelf setting where storms could be unable to erode deeply and to transport the echinoids basinward.

Alternatively taphonomic biases suggest that this accumulation could have originated during a period of sediment starvation ended by a sudden influx of obrutionary mud. As evidenced by Kidwell and Holland (2002) sediment accumulation at the scale of beds is highly episodic in most environments (timed with storms and floods, for example, rather than occurring steadily), and net rates of sediment accumulation are commonly slow in relation with the life span of individual organisms. Therefore, the skeletal remains of multiple generations typically become mixed within a single bed. This time-averaging of local but non contemporaneous remains is pervasive in the fossil record, particularly in the offshore environments as discussed by Norris (1986). However in the case of infaunal echinoids, such as *Brissopsis*, emergence at the sediment surface and

mass mortality (e.g. induced by hypoxic conditions) prior the definitive burial must have occurred.

5.3. Proximality trend in the origin and preservation of echinoid mass accumulations

Although all the three studied assemblages could be trace to storm-dominated distal shelf setting (from upper to lower offshore), there are differences in sedimentary structures and taphonomic features related both to increase in palaeobathymetric position and distance from shoreline.

Several studies evidenced expected changes in the sedimentary structures with the increasing of bathymetry.

Aigner and Reineck (1982) and Aigner (1985) evidenced that the sedimentary record in the siliciclastic shelves is mainly due to storm activity and denoted a proximal-distal trend in the nature of storm deposition from the shoreface to offshore environments. This trend consists in the change of thickness, granulometry and sedimentary structures of the storm layers. In the transition zone (upper offshore) shallower stormy facies are characterized by erosional bases, frequently paved by shell layers, parallel laminated sands, hummocky cross stratification and wave ripples (Fig. 63A1). More distal storm layers are thinner laminated sands and silts (graded rhytmites), the bases of which can be erosional (Fig. 63A2); shell layer are dominated by winnowed parautochthonous faunas. Finely laminated siltstones and massive, bioturbated, claystone could be considered deeper stormy facies (Figs. 63A3 and A4).

As for the taphonomic aspects, a general palaeobathymetric gradient in the preservational quality of regular echinoids were discussed by Kidwell and Baumiller (1990). These authors believe that in shallow water environments, above fair-weather wave base, the preservation potential of regular echinoids is lowest because of the carcasses can be likely physically reworked and fragmented. The best preservation is expected in the transition zone (upper offshore) between the fair weather and storm

wave base. In this zone, the immediacy and thickness of burial events, mainly related to storms, can prevent physical and biological reworking. In deeper open-shelf environments (lower offshore) the preservation potential of regular echinoids decrease because of storm deposition became sporadic and thinner and thus less effective in protecting the carcasses from biological disturbance (e.g. bioturbation).

This study evidenced a change in the features and origin of regular echinoid and spatangoid concentrations from upper to lower offshore environment. Regular echinoid accumulation of the Gesturi Marls originated in a environment where major storms can erode, transport and generate shell deposits (Fig. 63B), while the well preserved phymosomatid and spatangoid assemblages of Marmilla Formation generated in deeper (more distal) environment (lower offshore) characterized by rapid influx of very fine grained sediments without subsequent storm winnowing and reworking (Fig.63C).

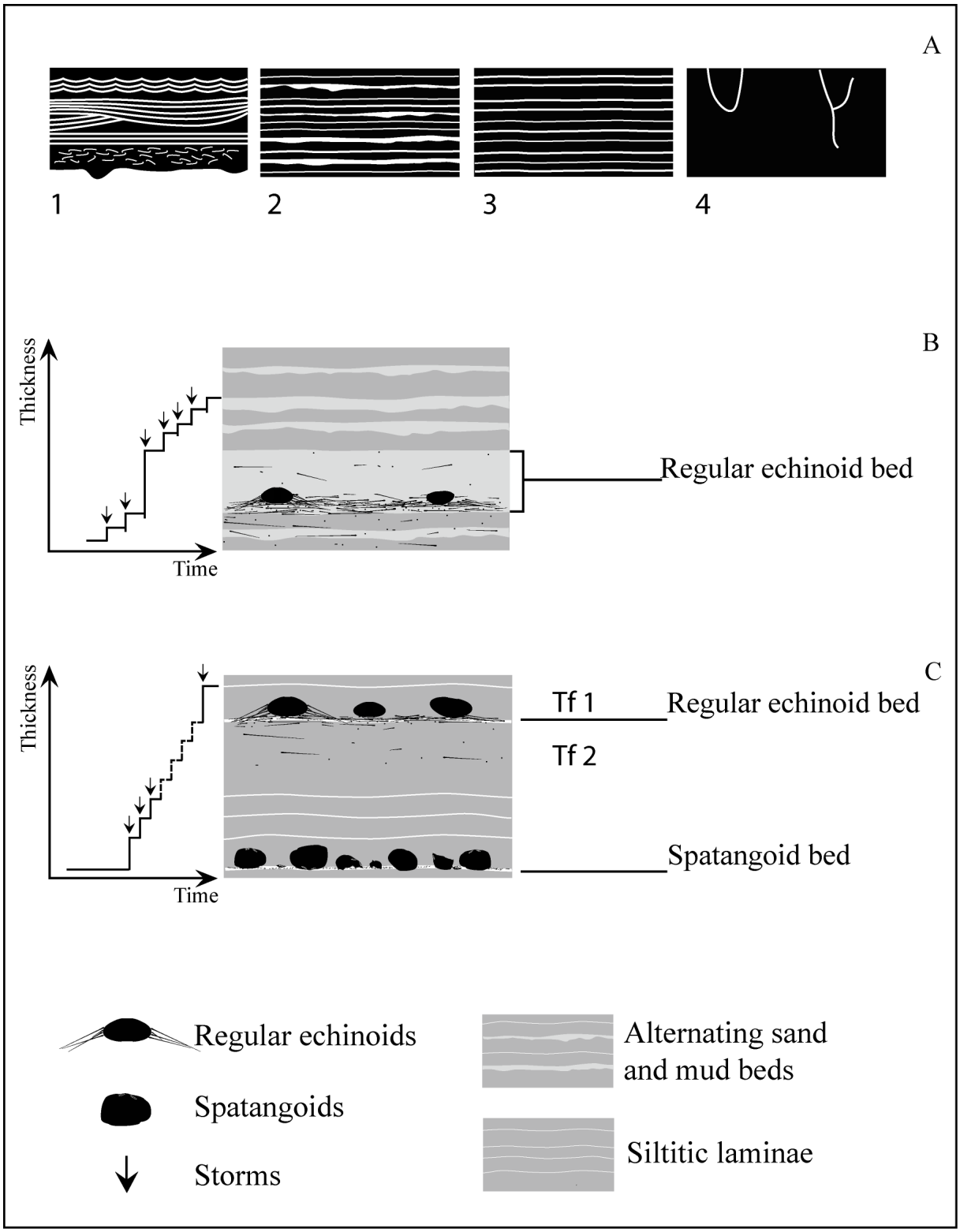
A
1
2
3
4
B
Thickness
Time
Regular echinoid bed
C
Thickness
Time
Tf 1
Regular echinoid bed
Tf 2
Spatangoid bed
Regular echinoids
Spatangoids
Storms
Alternating sand and mud beds
Siltitic laminae

Figure 63. A) Drawing based on the proximality-distality trend in offshore stormy facies as described by Aigner 1985. 1: facies characterized by erosional base paved by shell lag, planar lamination, HCS and wave ripples. 2: laminated sandy/silty alternations (graded rhytmites) 3: finely laminated silts; 4: massive bioturbated mudstone (fine siltstone and claystone).

B) The regular echinoid bed of Gesturi Marls originated in the distal part of the storm dominated upper offshore (transition zone) characterized by erosion, reworking and winnowing.

C) The origin of both physomatid and spatangoid mass accumulations took place in the lower offshore characterized by sediment starvation and rapid influx of fine grained sediments by storms.

Locality & Stratigraphy			
Locality	Gennas (Marmilla Formation)	Gennas (Marmilla Formation)	Ussana (Gesturi Marls)
Age	Lower Miocene	Lower Miocene	Middle Miocene
Sedimentary environment	Siliciclastic	Siliciclastic	Siliciclastic
Thickness of the accumulation	Single bed	Single bed	3 cm
Diversity and size variation			
Taxonomic composition	Monospecific (Regular echinoids)	Monospecific (Spatangoids)	Monospecific (Regular echinoids)
Sedimentary fabric			
Density	High	High	High
Spine orientation in plan view	Randomly oriented	Randomly oriented	Bi-directional oriented
Spine orientation in cross section			
Concordant	Dominant	Dominant	Dominant
Oblique	Present		Present
Perpendicular	Absenrt		Absent
Detailed taphonomy			
Test disarticulation	Low	Low to High	High
Spine disarticulation	Low to high	Low to High	High
Fragmentation	Low	Low to High	High
Abrasion	Absent	Absent	Absent
Encrustation	Absent	Absent	Absent
Post depositional features			
Skeletal mineralogy	Quartz		Calcite
Palaeoenvironment			
Interpreted environment of origin	Sublittoral	Sublittoral	Sublittoral
Interpreted environment of deposition	Sublittoral	Sublittoral	Sublittoral
Genesis of accumulation	Obrution	Time-average deposit	Tempestites

Table 3. Summary of taxonomic and taphonomic features of the regular echinoid and spatangoid assemblages.

5.4. Conclusions

1) Three echinoid mass occurrences from the distal shelf sediments of the Miocene of Sardinia were studied and compared.

2) In the Lower Burdigalian sediments of the Marmilla Formation two monospecific regular echinoid and one spatangoid mass occurrences were found. The regular echinoid assemblage consists of a dense accumulation of a new genus of phymosomatid, *Anisophyma*. The other echinoid assemblage is a monospecific *Brissopsis* bed.

3) The regular echinoid mass accumulation of the Gesturi Marls is a sea urchin spine bed with rare and poorly-preserved complete tests.

4) The echinoid concentrations are the results of a complex interplay of physical, sedimentological and ecological processes.

5) All the three studied echinoid deposits can be assigned to a storm-dominated offshore environment.

6) Observed variations in the taphonomic and sedimentologic features are due to three different genetic mechanisms:

The phymosomatid assemblage represents a rapid buried living high dense community (obrution).

The high dense *Brissopsis* assemblage is a time-averaged deposit by sediment starvation, buried by a rapid influx of mud flow.

The regular echinoid mass accumulation from the Gesturi Marls can be considered a tempestite event (Tab. 3).

7) The importance of these genetic mechanisms varied across the shelf and is related to palaeobathymetry and distance from the shoreline. The depositional environment of the echinoid beds within the Marmilla Formation was deeper marine than the echinoid bed from the Gesturi Marls and, therefore, was not subject to the same reworking intensity.

8) Proximality trend in the type of preservation (taphonomic features) was evidenced. The best preservation of regular echinoids occurs in the distal shelf setting (lower offshore) and is due to low energy environments (absence of reworking and winnowing) and rapid influx of fine grained sediments by storms.

9) Sedimentologic and taphonomic signatures of echinoid concentration beds can be used to infer depositional environments and relative water depth.

Chapter 6.

Systematic palaeontology

Class Echinoidea Leske, 1778

Subclass Euechinoidea Bronn, 1860

Infraclass Acroechinoidea Smith, 1981

Carinacea nov. [refers to shared presence of keeled teeth]

Calycina Gregory, 1900

Order Phymosomatoida Mortensen, 1904

Family Phymosomatidae Pomel, 1883

Genus *Anisophyma* n. gen.

Etymology – From *anisos* [Greek, meaning "being different"] because of its unique ambulacral structure (different from all other phymosomatids) and *phyma* [Greek, meaning "tumor"] in reference to its phymosomatid affinities.

Remarks – *Anisophyma* is closest to *Gautheria* and *Phymosoma*. In addition to the distinct ambulacral compounding it differs from *Phymosoma*: by its smaller mamelon (c. 20 % areole diameter instead of >30 % like in *Phymosoma*), by its lack of adoral pore crowing and adapical biseriality of ambulacral pores. From *Gauthieria* it differs by its flush peristome, by its straight ambulacral pore columns (distinct arcs in *Gautheria*).

Type species – *Anisophyma carlinoi* n.sp., designated herein.

***Anisophyma carlinoi* n. gen., n. sp.** (Fig. 64)

Diagnosis.

Etymology – Dedicated to Carlino Cabiddu, the man who first found the type locality of this species.

Types – Holotype is **(NHMW2013/0026/0001-a)**, from Gennas, Sardinia, Italy. Marmilla Formation, Lower Burdigalian, Lower Miocene. Paratypes **(NHMW2013/0026/0001-b,c,d)** have the same provenance as the holotype.

Description – Test size relatively small, with a test diameter (TD) ranging from 16 to 28 mm in the material studied. Outline circular, profile not preserved due to sediment compaction. The apical opening is large, ranging from 40 % of test diameter in small specimens to 44 % of test diameter in the largest ones. In outline the opening is pentagonal and extends slightly into interambulacrum 5. Its width is only slightly smaller than its length (92 to 95 %). The disc seems to have been slightly depressed below the level of the surrounding corona. No specimen retains the apical disc plates.

The ambulacra are about 26 to 28 % of test diameter at the ambitus and slightly narrower than the interambulacra. They taper gently aborally and orally. There appear to have been about ten plates per column at a test of 20-25 mm in diameter. Ambulacral plates are quadrigeminate orally and quinquegeminate aborally. Adorally, the structure is more complicated and involves a succession of single to trigeminate elements. Plate compounding is very unusual: it consists of an alternation of compound plates (tri- or quadrigeminate) with single elements that do not reach the perradial suture (except in the most adapical and adoral plates). The structure of the compound plates cannot be clearly seen. Ambulacral pores arranged uniserially and linear throughout, even at the

ambitus only weak arcs are formed. Pore pairs are oblique partitioned isopores with narrow attachment area (type P2 of Smith, 1979). Adorally neither pore crowding nor expansion of the pore zones is developed. Neither is there any biseriality adapically, even in the largest specimen (TD 25.2 mm). Each compound plate bears one large primary tubercle, straddling the demiplates of the compound plate, but not the interspersed single elements, which bear one large secondary tubercle only. The areoles of the primary tubercles are large, but not contiguous, being well separated from neighbour tubercles. The mamelon is relatively small, being only about 20% areole diameter wide in ambital plates. While ambital and aboral plates bear relatively few secondary and military tubercles, they are abundant on adoral plates. Both the primary and the secondary tubercles are crenulate and imperforate.

The interambulacra are slightly wider than the ambulacra at the ambitus (1.1 to 1.2 times as wide), only tapering slightly both adapically and adorally. Each plate bears one large primary tubercle which occupies most of the plate surface on ambital plates. Ambitally areoles are tangential, but not broadly confluent, adapically, in contrast they are smaller, separated from each other by a narrow band of military granules located along the adapical plate sutures. At the ambitus there are virtually no secondary tubercles, except a single one at each interradial triple junction. Adoral plates do carry considerably more secondary tubercles, the most prominent of which are located on the adradial margin of the plates, two or three to a plate. Likewise, there are numerous military tubercles, but only the larger ones of these are well visible in the present material. Adapically, there appears to be a naked interradial zone which is slightly depressed. Like those of the ambulacra, the tubercles are crenulated and imperforate and have a small mamelon (about 18-20% areole diameter).

The peristome is circular, not invaginated and relatively small, ranging from 29 to 33% of test diameter. Buccal notches are not readily apparent and were small and insignificant. The perignatic girdle is not preserved.

Lantern. The demipyramids are poorly preserved but are compatible with a stirodont or camarodont lantern-type. The teeth are keeled. The rotulae show a trapezoidal condylus which is broadly connected to the adaxial part of the rotula. Epiphyses and compass elements could not be identified in the jumbled masses of lantern parts.

Spines. The primary spines are slender and long (up to 60 mm), exceeding twice the test diameter in length. The base is well defined with a crenulate acetabulum, distinct milled ring and striated collar. The lower shaft is smooth and unornamented, whereas the distal two thirds of the shaft are ornamented by faint and widely spaced longitudinal ridges. The spines taper only slightly distally and end in a bluntly rounded point. Internal structure not preserved, but the sharp difference between collar and shaft indicates that a cortex layer is present. Secondary spines are shorter, 5 to 10 mm in length, and very thin. They have a marked base, with distinct milled ring and very short collar. Their shaft is finely striated. Distally they are tapering slightly towards a blunt, rounded point.

Occurrence – The type material is found in the locality Gennas, 1 Km South of Villanovaforru (central Sardinia), within the Marmilla Formation (Lower Burdigalian).

Discussion – The ambulacral compounding is slightly reminiscent of that of *Gauthieria radiate* (Sorignet, 1850) (see Smith and Wright, 1996: text-fig. 104). The latter has quinquegeminate compound plates consisting of triads with a common straight-edged and unbroken perradial wedge and two simple plates reaching the perradius, one above and one below the triad. In *Anisophyma carlinoi*, there is a single simple plate per compound plate only. Additionally, these simple plates reach the perradius only in the

most adapical and adoral compound plates, whereas they are restricted to the adradius in ambital plates. Unfortunately, the compounding structure of the large element cannot be clearly seen in *Anisophyma*. Aborally, it appears to consist of an upper and lower element reaching the perradius and one or two central demiplates restricted to the adradius. Subambitally, however, it appears to invole a lower element transformed into a demiplate.

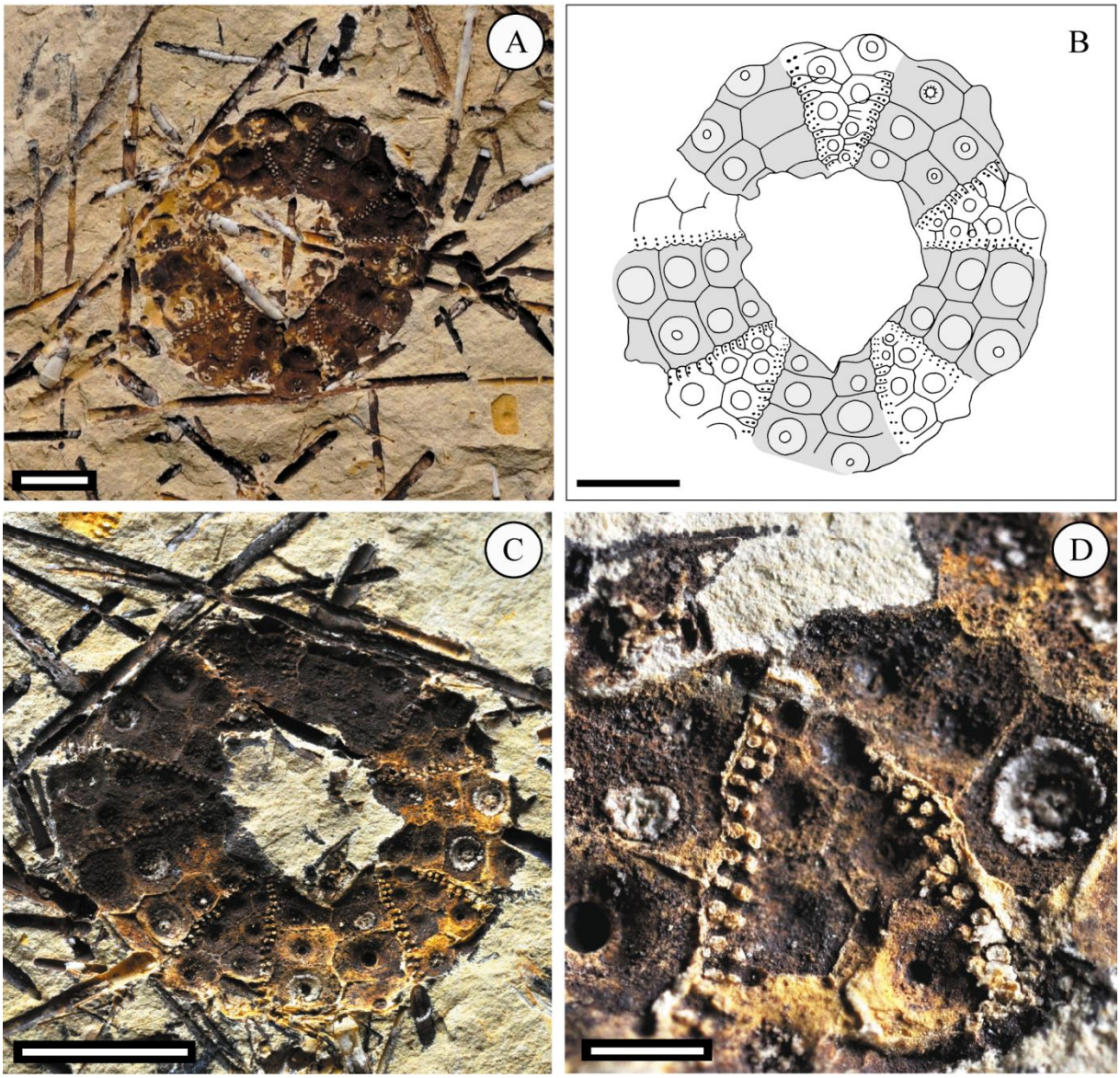

Figure 64. *Anisophyma carlinoi* n.gen n.sp.: A) Holotype NHMW2013/0026/0001-a, apical view; B) Camera lucida drawing of holotype, apical view; bar represents 5 mm. C) Specimen MDLCA23522; bar represents 10 mm. D) Detailed of ambulacral plates of the specimens MDLCA23522; bar represents 2 mm.

General Conclusions

1) The taphonomic and sedimentologic study of multi-element skeleton accumulations allowed to shed light on their origin and palaeoecology.
2) Functional morphology, palaeoecology and sedimentation rates are the three main factors that guide the genetic interpretation of these fossil accumulations.
3) Shell accumulations originated through a wide variety of processes, including proximal and distal storm events, multiple in situ reworking, authocthonous accumulation and obrution.
4) It should be recognized that the genetic processes described in this work represent a limited range of a wide variety of mechanisms which can produce well-preserved fossil accumulations.
5) The origin of mass accumulations in shallow water environment can be promoted by sediment movements, rapid burial and physical concentration of skeletal material through transport, winnowing, reworking and amalgamation. Therefore test architecture and physical factors play the main role in the origin of well-preserved fossil deposits. Nearshore depositional environments are dominated by sedimentological concentrations but can also include sedimentologically overprinted biological concentrations.
6) Sedimentation is more episodically in deeper water environments (particularly in the lower offshore) mainly due to intermittent storm deposition. Shell-bed development mainly can be the results of ecologic (biologic) mechanisms, shell accumulation during episodes of sediment starvation and rapid burial by storm events.
7) The analysis of multi-element skeleton mass accumulations shows that these fossil deposits are a useful tool for palaeoenvironmental and palaeoecological reconstructions.

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